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Obligatory and Facultative Insects in Rose Hips

Their Recognition and Bionomics

W. V. BALDUF

ILLINOIS BIOLOGICAL MONOGRAPHS: *Number 26*

THE UNIVERSITY OF ILLINOIS PRESS
URBANA, 1959

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INTRODUCTION

For some years, my daily walks between home and office took me past a fine stand of *Rosa rugosa* growing northwest of the "Old Ag. Building" on the University campus at Urbana, Illinois. Here, in the mid-twenties I discovered a red-and-black beetle boring into rose buds with its long beak. During the ensuing years I permitted my interest to extend only to the accumulation of the earliest dates of its annual appearance, presuming that so common a species had certainly already been studied adequately. Then in mid-June of 1943, I found several honey-yellow chalcids, new to me, engaged in inserting their long terebras into the young hips of this rose. My guess was that they were parasitizing some other insect in the hip—possibly the larva of the snout beetle. Seeking to gain data about the geographical range of this chalcid, I picked some hips of *R. acicularis* at "Eaglesnest," in northern Minnesota, on September 17, 1943. Upon opening the package at Urbana on October 7, I was surprised to find seven stramineous dipterous puparia that had obviously developed from larvae formerly resident in the hips. While removing many such larvae from hips at Eaglesnest in August of 1944, I made the acquaintance of a small caterpillar that shared the fleshy coat of the hips with the dipterous larva.

Thus, by August, 1944, I had learned that rose hips in Minnesota and Illinois are sometimes inhabited by four phytophagous species of insects. These proved to be the rose snout beetle, *Rhynchites bicolor* (Fabr.), Curculionidae; the American rose hip fly, *Rhagoletis basiola* (O.S.), Trypetidae; the cherry fruitworm, *Cydia (Grapholitha) packardi* (Zell.), Olethreutidae, and the American rose seed chalcid, *Megastigmus nigrovariegatus* Ashm., Torymidae. In later years, the European rose seed chalcid, *M. aculeatus* (Swed.), was reared from hips obtained from Illinois and states to the east.

But these phytophagous residents of rose hips later proved to constitute only the smaller portion of the inhabitants more or less characteristic of this microhabitat. From 1944 to 1953, an impressive series of parasitic Hymenoptera, several new to man, were obtained from the above phytophags. The facts in their lives were learned insofar as permitted by the limits of my time as a teacher and the amounts of host and parasite material available.

Since the hips and insects processed in that decade originated principally in Minnesota, Wisconsin, and Illinois, with fewer samples from other northern states, it is probable that still other phytophags and para-

sites utilize rose hips as food or shelter, particularly in more southerly and westerly areas of the United States. Not only may further investigation add more species to the list, but it will certainly serve to further clarify the modes of life and roles of certain species found only in small numbers to date. Perusal of the literature has revealed several additional "hip insects" native to Europe and Russia.

The principal objectives were to learn what species of insects depend more or less on rose hips for food and/or shelter, their bionomic relations to the hip or to each other, and the life histories of each species. These goals were reached to varying degrees, depending chiefly on the quantities of living material available for investigation. No instruments were employed to determine the influence of temperatures and relative humidities on the crops of hips or the development and populations of the insect species. Exhaustive technical descriptions have not been included for most adult and immature stages of the insects found in or upon the hips. Such studies of the immature stages may properly constitute the subject matter of another treatise. The characteristics described are believed adequate to enable interested persons to distinguish the several stages of any one species from those of others.

Samples of hips from 32 species or varieties of roses were processed in the course of this work. While the bulk of the materials originated in Minnesota, Wisconsin and Illinois, from *Rosa acicularis*, *R. blanda*, and *R. carolina*, I collected other lots of hips from Ohio and Indiana, and received shipments from cooperating persons in Washington, Idaho, California, Maine, New York, Virginia, North Carolina, Mississippi, Texas, Nebraska, Kansas, Iowa, and Alaska, as well as in Saskatchewan, Manitoba, and Ontario. Approximately 14,000 adult specimens of rose hip insects were reared, and additional thousands of larvae of the phytophagous species have been dissected to obtain the endoparasitic larvae, of which numerous specimens are preserved in alcohol.

Altogether, about 45 species of animals—Insects excepting an acarid mite and an annelid worm—were found to be associated with rose hips. They are divisible into three groups according to the nature of their bionomic relations to the hips; namely, incidental, facultative and obligatory. The incidental forms, being paurometabolous and physically not adapted for life within the hip, occasionally visit the hips to feed, or to attach or insert their eggs, but also utilize other similar hosts to perform these functions. About 15 species fall into this category, and are not treated in the present monograph.

The facultative and obligate groups comprise only holometabolous insects, and their bionomics constitutes most of the subject matter of this treatise. Their more or less legless, or adaptive, larvae reside, feed, and develop out of sight within some part of the rose hip. Present knowl-

edge of their host relations shows that certain of these Holometabola confine themselves to rose hips, developing in no other plants, or parts of plants. Such obligatory species are *Rhagoletis*, *Rhynchites* and *Megastigmus*; *Opius* and *Halticoptera*, endoparasites of *Rhagoletis*; and *Luchatema*, an internal parasite of *Rhynchites*.

By contrast, it is well known that some other Holometabola also pass their larval life in plants other than *Rosa*. Such facultative members of the rose hip complex are the cherry fruitworm, *Cydia packardi*, which also inhabits apple, cherry and blueberry, and the parasites *Glypta*, *Scambus* and *Euderus* on the cherry fruitworm, and *Bracon*, whose host list includes, beside *Rhynchites*, many coleopterous and lepidopterous phytophags of similar habit in plants other than rose.

Besides suggesting the nature of the subject matter contained herein, the main title is intended to imply my conviction that all bionomic material regarding the species is properly included whether it relates to rose hips directly or to alternate host plants and host insects.

The bionomic data pertinent to the species of the rose hip community were obtained by four simple methods. First, direct observations in the field yielded records on seasonal occurrences of the adult insects, and information on the activities of mating, oviposition, feeding and movement. Second, dissection of samples of immature hips at intervals of 10 days was a means of learning the typical niches of the several phytophagous insect larvae and their ectoparasites, their developmental pattern in the course of the season, and variations in populations with reference to year, locality and species of rose or insect host. In turn, dissections of the phytophags yielded similar information as to their endoparasites. Third, in September and October quantities of more or less ripe hips, gathered in various northern states, Alaska, and Canada, were stored, mostly at Urbana, Illinois. Cloth covers placed on the glass "hip jars" prevented both excessive drying of the hips and escape of the emerged larvae and adults of the ectoparasites. The larvae were removed, usually on the day of their exit from the hips, and either preserved for subsequent description and identification, dissected in order to trace the later developmental aspects of the endoparasites, or transferred to rearing cages designed to yield the pupal and adult forms. Fourth, four-inch flower pots, filled with soil and surmounted with old-fashioned lantern globes closed above with fine-meshed cloth, constituted cages suitable for rearing the rose hip fly and the rose curculio and several species of endoparasites. The curculionid larvae readily enter the soil, where they winter; puparia of the *Rhagoletis* winter fairly well when placed between two discs of cloth on the surface of the soil. The pots, minus the chimneys, were set out-of-doors, countersunk in the ground,

under natural conditions from November to May, then taken into an open shelter and topped with the chimneys to await the emergence of the adult beetles, flies or hymenopterous parasites.

While some cherry fruitworms survived the winter among hips in jars, better results could probably have been secured had pithy plant stems been provided for the larvae to enter for preparation of their hibernacula. Both species of the rose seed chalcids winter as matured larvae in the achenes, and the adults may be reared readily in the spring from hips stored in glass jars. Mould growing profusely on the decomposing moist hips appeared not to affect adversely the development of the chalcids, whereas extreme hardening through desiccation seems to have blocked the emergence of some adults.

The ectoparasites of *Cydia* and *Rhynchites* pupate in the hips. Accordingly, the adults of these emerged in the hip jars. Since some individuals or species emerge in the spring, the hips need to be kept under observation during the winter. Valuable host-parasite data were obtained by isolating in vials the ectoparasitized hosts in the hips until the parasitic larva or pupa became adult.

Acknowledgments

In a comprehensive project such as this, the investigator is dependent, to a degree, on other persons for funds, performance of routine duties, acquisitions of live material from outlying areas and for the technical services of specialists in the identification of plants and insects. I am pleased to acknowledge all such aids with appreciative thanks, even though space does not permit the naming of all individuals concerned.

The research board of the Graduate College of the University of Illinois provided funds for preparation of drawings, bibliographical work, care of rearing cages, for pinning, labeling, and arranging many adult specimens reared, and typing a part of the manuscript. The drawings were made by Donald Van Horn, then a graduate student in zoology.

Quantities of rose hips were gathered at the places and by the persons named herewith, and mailed to me for processing. Alaska: S. E. Lienk, C. O. Esselbaugh, Katherine Sommerman. Saskatoon, Saskatchewan: Mrs. Arni Arnason. Manitoba: R. D. Bird. Ottawa, Ontario: T. N. Freeman. California: Albany and Berkeley, R. F. Smith and J. W. McSwain; Cedarville, Sam Rea. Washington: Spokane, Pullman, and Wawawai; and Moscow, Idaho, C. O. Esselbaugh. Utah: Mapleton, C. E. Hopla; Mt. Timpanogos, Utah County, C. L. Hayward. Kansas: Manhattan, R. H. Painter. Nebraska: Crete, W. F. Rapp. Oklahoma: Norman, H. P. Brown. Missouri: Ironton, David Lauck. Minnesota: Cook County, Mr. and Mrs. Edgar Love, Katherine Love; Ely, Mr. and Mrs. Jalmer Lake. North Carolina: Ash, Guilford and Transylvania Counties, and Raleigh, W. B.

Fox, Ohio: East Liberty, A. J. Sharp; West Alexandria, R. T. Bell, New York: Geneva, S. E. Lienk, Maine: Orono, F. H. Lathrop, Virginia: East Falls Church, L. H. Weld, Illinois: Rochelle, S. E. Lienk, John Porter, Seward and Lanark, J. Porter; Alton, David Lauck; West Frankfort, Wayne Carlisle; San Jose, D. M. Tuttle; Rising, C. E. Wester; Philo, Mr. and Mrs. F. H. White.

I received 12 lots of wild rose hips through the cooperation of Wilbur A. Rush, Chief, Division of Lands and Waters, Iowa State Conservation Commission. These were secured by twelve members of his field staff in their respective areas of supervision. Also, four samples came to me by courtesy of the Colorado Forestry and Horticulture Association, Denver.

The hips involved in the course of this investigation represent approximately 30 species or varieties of roses. Taxonomic interpretation differs somewhat among students of the genus, which botanists generally recognize as a difficult one to determine. For their painstaking work in identifying most of my rose materials, I am indebted to Dr. John W. Moore, then botanist at the University of Minnesota, and Dr. G. Neville Jones, systematic botanist at the University of Illinois. Some materials were named by the late Dr. L. R. Tehon, Illinois State Natural History Survey; Dr. E. L. Stover, Eastern Illinois State College, Charleston; the late Messrs. James S. Hutchinson and S. W. Hall, University of Illinois. The following botanists identified the roses growing in the areas of their residence: Dr. B. F. Harrison, Brigham Young University, Provo, Utah; Dr. R. C. Russell, University of Saskatchewan, Saskatoon; Prof. Fay Highland, University of Maine, Orono; Prof. W. B. Fox, North Carolina State College, Raleigh; Dr. C. F. Gates, Kansas State Agricultural College, Manhattan. The hips received from Fairbanks, Alaska, had been determined by Father Le Page, according to Dr. S. E. Lienk, who sent them to me.

I am indebted also to Dr. G. Neville Jones, University of Illinois, and Dr. Reino O. Alava, rosarian of the Missouri Botanical Gardens, St. Louis, for checking the scientific names of all plants mentioned herein, with reference to the accepted status of specific and subspecific nomials, specific synonyms and names of authorities insofar as this was possible within a genus so involved as *Rosa*. Dr. Leland Shanor, mycologist, then at the University of Illinois, identified a fungus parasitic on larvae of the rose curculio.

The insects and other invertebrates observed in the course of this study were identified by the following staff specialists who are, or were, at the United States National Museum, Washington, D.C.: Diptera, Alan Stone and C. W. Sabrosky; Chalcidoidea, A. B. Gahan and B. D. Burks; Braconidae, C. F. W. Muesebeck; Ichneumonidae, H. K. Townes and

Luella M. Walkley; Lepidoptera, H. W. Capps, J. F. Gates Clarke and the late Carl Heinrich; larvae of Cleridae, O. L. Cartwright, and Acaridae by E. W. Baker.

L. J. Stannard, Illinois State Natural History Survey, determined some lots of mites, and L. J. Thomas, University of Illinois, identified the annelid worm, *Chaetogaster* sp., which I have from *Rhynchites*.

I am indebted to The Ohio State University for the loan of the doctoral thesis of N. D. Blackburn (1944), and to the author for permission to use some of the original unpublished material from the thesis: also to the University of Wisconsin and Dr. D. A. Dever (1953) for like favors.

Special thanks are merited by my wife, Willma, for her interest, patience, and assistance. She willingly permitted me to convert the back porch of our home into an insectary and laboratory in order to bring my night work of several years conveniently to hand. She also mounted thousands of specimens on pins.

THE ROSE HIP FLIES, TRYPETIDAE, DIPTERA

As interpreted today, at least three species of trypetid flies are known to develop as larvae in the fleshy hypanthium of rose hips. They are *Carpomyia Schineri* (Loew), *Rhagoletis alternata* (Fallén) and *Rhagoletis basiola* (Osten Sacken).

Carpomyia Schineri (Loew)

Loew (1862) described this species under the name *Oedaspis Schineri*. It is cited in the literature also with the generic names *Trypeta* and *Orellia*. According to Hendel (1927) and Seguy (1934), it occurs throughout central and eastern Europe. The species has been of minor importance as a pest, and there is relatively little information at hand about its mode of life. Rodendorf (1938) includes the species in a key to a number of Trypetidae that are most often found in fruits at quarantine stations in Russia. It has three relatives that have attracted some notice owing to their injury to fruits—*C. incompleta* Beck (Rodriguez, 1926) and *C. vesuviana* A. Costa (Khare, 1923) for their attack on berries of *Zizyphus*, and *C. caucasica* Zaitz (Prinz, 1919) as a pest in melons. These I regard as significant here because their habits are perhaps indicative of those of *C. Schineri*.

Eppelsheim (1871) apparently was first to discover the host plant of *C. Schineri*. He reared adults from larvae found in the hips of *Rosa spinosissima* at Grünstadt near Speyer and Heidelberg in the Rheinland-Pfalz, Germany. One adult, reared in 1872, was sent to Jos. Mik (1898)

and a fine series to Kaltenbach (1874). Perris (1876) reported finding a "very large" dipterous larva in the overripe hips of *Rosa canina*. He gathered a quantity of hips and reared many such larvae from them, later obtaining adults, which he identified as *C. Schineri* with the help of M. Gobert and the literature of Schiner. These specimens were obtained around Mont-de-Marsan, north of the river Adour in the province of Gascony, in southwestern France. Von Röder (1891) added another species, *Rosa gallica damascena*, to the host list, based on adult insects that he received from Dr. G. Dieck in Zöschen, near Merseburg, who reared them from the fruits.

Eppelsheim observed the mature larvae to leave the hips in August. Those reported by Perris emerged after mid-September. These observers agreed that the larva descended to, or into, the soil where they puparated in the fall. The adult flies emerged from the puparia in the following June (Eppelsheim), and beginning with the last days of June, to July 10, 1875 (Perris). While oviposition seems not to have been observed, it may safely be assumed that the fly inserted the eggs into the hypanthium. The larvae ate out winding galleries in the flesh of the hip and did not disturb the stony seeds within it (Eppelsheim). No parasites were recorded in the literature cited.

Rhagoletis alternata (Fallén)

Rhag. alternata, known to European entomologists since Fallén described it in 1820, and *Rhag. basiola* are very similar in their physical characteristics and apparently also in their modes of life. As a consequence, some doubt remains concerning their taxonomic status. For the present purpose, I am adopting the view of Alan Stone (1951) that it seems better for now to consider them as distinct species. In Germany, *Rhag. alternata* is called *die Hagebuttenfliege*; in Sweden, *Nyponflugan*.

Distribution and hosts. *Rhag. alternata* is widespread in Europe, and has been reported from the hips of many species of *Rosa*. Following are the records known to me: *Rosa canina*, middle and northern Europe (Hendel, 1927); Surrey County, England (Niblett, 1936), Scotland (J. Hardy, 1873); *R. villosa*, south of the Alps (Hendel, 1927), and Scotland (J. Hardy, 1873); *R. rugosa*, Kiev, Russia (Belski, 1924); *R. hugonis*, England (Collin, 1947); *R. spinosissima*, Grünstadt, Germany (Eppelsheim, 1871); *Rosa* spp. not determined, Austria (Schiner, 1864), Koblenz, Germany (Klein-Krautheim, 1937), England (Pearce, 1928), Ireland (Wilson, 1931), and Sweden (Anon., 1941).

Wilson (1935) obtained this fly from the following 27 forms of *Rosa* in the gardens of the Royal Horticultural Society at Wisley, England: *Rosa alpina* var. *pyrenaica*; *blanda*; *calocarpa*; *canina*, vars.; *Chaberti*; *cinnamomea*; *feneliensis*; *glauca*; *gymnocarpa*; *lucida*; *macrantha*; *mollis*;

*sima; moschata, var. *alba*; *Moyesii*; *multibracteata*; *nutkana*; *oxyodon*; *parviflora*; *pomifera*; *eglanteria*; *rubrifolia*; *rugosa*; *Selongiana*; *sericea*; *swenginzowii*; *virginica*; *woodsii*.*

Without knowledge of the food plant, *Rhag. alternata* has been recorded also from the Piedmont, Italy (Rondani, 1870); France (Gobert, 1887); Boitsfort, Belgium (Guilliaume, 1904); Kiel, Germany (Boie, 1847), Swinemünde and Berlin (Zacher, 1919), Berlin-Buch. (U.S. National Museum); and Maribo, Denmark (U.S. National Museum). Fallén (1820), who named this fly, *Rhag. alternata*, gave its "habitat" as Esperöd Scaniae, Sweden. The United States National Museum also has specimens from hips sent from Sweden and intercepted at Cleveland and New York in 1947 and 1948.

In addition to the above records of *Rhag. alternata* from *Rosa* spp., the literature contains three reports of its occurrence in other plants. However, the latter three are now known to be in error. These cases are reviewed briefly.

Von Roser (1834, 1840) stated he had *Rhag. alternata* from the fruits of *Lonicera xylosteum* L. Subsequently Mik (1898), Loew (1862) and Klein-Krautheim (1937) showed that von Roser actually had two species of Tryptidae from these fruits—*Rhag. cerasi* L. and *Acidia speciosa* Lw.—and that he had mistaken *A. speciosa* for *Rhag. alternata*.

Fletcher (1883) reported *Rhag. alternata* as having been obtained by J. B. Hodgkinson from mines in the leaves of *Impatiens nolitangere* L. Fletcher (1883a) later corrected the error. Hodgkinson had inadvertently thrown mined leaves of *Impatiens* and rose hips together in his greenhouse. Unaware that the hips contained dipterous larvae, he supposed the flies to have originated in the leaf mines.

A third error in host records is obviously due to confusion on the part of the abstracter of the article by Zacher (1916) in the *Review of Applied Entomology*, Series A, 8(1920):288. Here it is stated that Zacher found the tryptid "Zonosema alternata (Fall.)" infesting barley. Scrutiny of the original article showed that the fly attacking barley was a chloropid, *Lasiosina cinctipes* Meig., and that Zacher reported *Rhag. alternata* from rose hips.

Food of the larva. That the larvae inhabit rose hips, and, when mature, emerge from them, has been long known in Europe. This has sometimes led to the incorrect assumption that the larvae inhabit the seed cavity and feed on the "seeds," i.e., achenes, thereby injuring them. The occurrence of puparia among rose seeds, reported by Wilson (1931), was probably due to the artificial conditions in which the inhabited hips were stored, and would not be found in nature. However, the belief that the larvae consume or injure the achenes has persisted until recent years. In the abstract of an article by Reichert (1935), the *Review of*

Applied Entomology, A, 23:506, represents him as stating that the larva injures the seeds in the hip. Klein-Krautheim (1937), in reviewing some published statements on this point, noted that Mik (1898) assumed that the seeds were injured, whereas such attack was disclaimed by Luce (1898). In his own studies, Klein-Krautheim found that the larvae do not feed on the seeds. If the food habits of *Rhag. alternata* are like those of its very close relative, *Rhag. basiola*, the larvae limit both their feeding and residence to the hypanthium.

Damage to rose hips. As the feeding larvae mine the hypanthium, the normally green or red hip becomes discolored with brown to black strips or blotches, and as more of the tissue is consumed by the larger larvae, the hypanthium collapses and wrinkles. Zacher (1919) cited destruction of the entire crops of hips at Swinemünde in 1915 and previous years, and at the Biologisches Reichsanstalt in Berlin in 1918. In the latter case, all that remained on the rose plants in August were the hip petioles and tattered scanty remnants of the fruit flesh. Remnants of the larger hips at the tops of the plants, including the achenes, had fallen to the ground. Presence of the larvae in hips still hanging on the plants was indicated by the dull red patches over the feeding burrows.

Vitamin C content of rose hips. In recent decades, and particularly during World War II, the hypanthium of the rose hip was found to be an important source of ascorbic acid or vitamin C, valuable in human nutrition. Consequently, *Rhag. alternata* came to be regarded as a pest in some Eurasian countries. An anonymous article, entitled "Nyponflugan" (1941), reported interest in vitamins of rose hips in Sweden, and briefly described the life cycle of this enemy fly. Belski (1924) compiled a list of "pests" of medicinal plants occurring in the vicinity of Kiev, Russia, and included *Rhag. alternata* as one of the enemies of rose hips, which he regarded as medicinal because of their vitamin C content. Through personal correspondence with a resident of Canada, I learned that the Canadian government was urging its citizens to utilize rose hips as an available source of ascorbic acid. Subsequently, Melville and Pyke (1947) investigated the relation of specific variability and the environment on the content of vitamin C in English rose hips. Wilson (1935) had found that this fly develops in 27 species and varieties of roses in England. Hence, the destructive larva has gained economic significance in that country. The extensive damage reported by Zacher (1919) indicated that this fly sometimes had a similarly detrimental effect on the yield of rose hips as this source of the vitamin in Germany.

Life cycle and habits. Bouché's report in 1834 apparently derived entirely from his own observations. In Germany, during the summer he found the larvae eating out tunnels in the "envelope" or hypanthium of

Rosa villosa, thereby destroying its "fruits." Late in August, the larvae descended into the ground, where they pupariated, and in June of the next year, the adults emerged from the ground. Thus, Bouché concluded that *Rhag. alternata* can, and does, complete only one cycle or generation in a year.

Some of these facts had also been reported by Eppelsheim (1871), J. Hardy (1873), and Kaltenbach (1874), and further observations were made by Zacher (1919), Wilson (1935), Niblett (1936), and Klein-Krautheim (1937). Adult flies remained alive 5 to 16 days when Klein-Krautheim supplied them with moistened sugar. He observed that copulation in captivity sometimes continued uninterrupted for at least 2 hours. Search of the literature has revealed no statement regarding oviposition, but it may be assumed that *Rhag. alternata* inserts the eggs singly into the hypanthium, as its close relative, *Rhag. basiola*, is known to do. The early instars apparently have not been described. Collections by various investigators from mid-August to October have shown that the larvae of *Rhag. alternata* mature and emerge from the hips from August (Bouché, 1834; Eppelsheim, 1871) to November (J. Hardy, 1873), breaking through the skin of the hips to escape. J. Hardy (1873) was obviously in error in stating that the hips show the openings by which the maggots gain access; and also where he added that the larva appears not to confine itself to a single fruit, and readily enters a fresh one when presented to it. He possibly had reference to the entrance of matured emerged larvae into hips stored in captivity, where the normal soil medium for pupariation was lacking.

Pupariation has been observed by writers quoted above to take place from a few hours to a few days after the larvae issue from the hips. J. Hardy (1873) commented that the "puparia were mostly cemented to the object, on which they lay, by a moisture exuded from the vent." Fraenkel and Brooks (1953) describe the same phenomenon in other Diptera, but have shown that the cement issues from the mouth. In describing *Rhag. alternata*, writers agree that the larvae normally pupariate on or in the soil, and that the puparia constitute the over-wintering stage. But whether the insect is a prepupa or a pupa in this season seems not to have been ascertained. The adults reportedly issue the following year, chiefly in June.

Additional data on habits and development are given by Klein-Krautheim (1937) and Niblett (1936). At Giessen, Germany on October 7, 1933, Klein-Krautheim (1937) received a quantity of the hips of *Rosa canina* from Koblenz. Larvae emerged on and after October 8, but some had issued previously. Puparia kept in a cool room yielded males and females, April 4 to June 9, 1934. At Surrey, England, Niblett (1936) obtained a lot of the hips of *R. canina* on October 13, 1934. Larvae began

emerging the next day, and adults issued from the resulting puparia June 5-21, 1935. A second lot of puparia observed by Niblett (1936) originated in the hips of *Rosa hugonis*. They yielded flies during the first week of the next June.

Klein-Krautheim (1937) noted that when their cage stood in sunshine the flies ran and flew about in a lively manner. When walking, they made rowing movements with the wings such as are characteristic of the Trypetidae and related flies. Klein-Krautheim presented a hypothetical chronology of the life stages, based on his observations on *Rhag. alternata* and data from the literature on this and other species of *Rhagoletis*. This hypothesis holds that *Rhag. alternata* passes its larval life in the hips of roses, emerges to pupariate in the fall, and winters as a puparium, thus completing one life cycle in a year.

No reports have been found in the literature concerning parasites on any stage of *Rhag. alternata*.

Rhagoletis basiola (Osten Sacken)

This is the fruit fly found in the hips of roses in North America. According to Stone (1951) it is known in the literature under several generic and specific names.

Distribution. My records from the literature (Osten Sacken, 1877; Doane, 1899; Gibson, 1915; Robertson, 1923; Crane, 1932; V. T. Phillips, 1946), the U.S. National Museum, and my own rearings show that *Rhag. basiola* occurs from near the 35th line of latitude in the United States to near the Arctic Circle in Alaska, and from the Atlantic to the Pacific oceans. Its distribution appears, therefore, to be coextensive with that of the genus *Rosa* as represented by its wild-growing species. It is doubtlessly true that the acquisitions of additional records from the collections of other scientific institutions would serve to intensify but not materially extend the limits of its known range. All the southern provinces of Canada are represented, but I have no records for 13 states that lie wholly north of latitude 35°.

More specifically, the extreme northern limit of its occurrence is represented by flies reared from hips sent to me by S. E. Lienk and C. O. Esselbaugh from 12 localities in northwestern Canada and Alaska along the Alcan, Richardson, and Steese highways. Miller House, located about 66 miles south of the Arctic Circle, is the presently known northernmost point of its occurrence. On the other hand, San Luis Obispo, California, Las Vegas, New Mexico, and North Carolina are the southernmost points for which I have records. A challenging distributional problem is posed by the lack of reports for southern United States. If *Rhag. basiola* actually wanes southward, what may be the factors that cause it to do so?

Hosts. Records from the literature cited above, from the U.S. National

Museum, and, for the most part, from my own rearings give a total of 19 species of *Rosa* now known to be hosts of *Rhag. basiola*. They are listed here with the geographical localities where the fly has been obtained from them: *Rosa acicularis*, northwest Canada and Alaska; *R. acicularis*, *blanda* and *Macounii*, northeastern counties of Minnesota, north of Lake Superior; *R. blanda*, *carolina* and *arkansana*, Wisconsin; *R. Macounii*, *woodsii*, *nutkana*, *alcea* and *pyrifera*, British Columbia, Saskatchewan and Manitoba; *R. Macounii*, Nebraska; *R. woodsii*, Utah; *R. blanda*, Ottawa, Ontario; *R. spaldingii*, *nutkana*, and *ultramontana*, northwestern United States; *R. rugosa*, Rhode Island and New York; *R. nitida* and *virginiana*, Orono, Maine; *R. eglanteria*, North Carolina; *R. canina*, *palustris*, *gallica*, *setifera* and *carolina*, Ohio, Indiana and Illinois.

I made no systematic search in nature for other plants *Rhag. basiola* may inhabit. Had the fly any other hosts except *Rosa*, some of these would almost certainly have been discovered and reported in the course of earlier investigations on insect pests of rosaceous fruits.

Adult (Fig. 1). Males, 3.8 to 5.7 mm., usually 5.2 to 5.5 mm.; females, 4.2 to 6.2 mm., mostly 5.0 to 6.0 mm. long. Dorsum of body largely dull orange, rest of body and the legs varying in shades of yellow. Postscutellum with a pair of black marks sometimes extending to metanotum. Body generally smooth, shiny; hairs and bristles moderately dense. Wings (Fig. 3) with a somewhat variable pattern of brownish black areas and bands, but "apical dark spot . . . usually joined to the subapical transverse band or narrowly separated" (Stone, 1951, Fig. 3). In the female, exposed apical abdominal segment trapezoidal, more rigid than preceding segment, and, in life, darker, brownish. Ovipositor consisting of three tapering terminal segments telescoped into abdomen when not in use, the distal one hard, pointed for penetration of rose hips. In male, genital segment subspherical, bearing a short, soft, pale, median capitate process and a pair of flat, tapering, firm, diverging orangish brown claspers usually held directed forward in contact with venter of abdomen.

Egg (Fig. 2). As it occurs naturally in the hypanthium of the rose hip, the egg consists of two structurally distinct parts, the egg proper—composed of chorion, embryonic membrane and yolk or embryo—and a cap borne on the caudal end of the egg. The egg as a unit, including the cap, varies from 1.0 to 1.25 mm. in length, but usually is 1.2 mm.; at its widest point it is about one-third as broad as it is long, and considerably broader than deep. In form, the egg proper is elongate-oval lengthwise, oval also in its transverse diameter, moderately rounded at both ends but more sharply so at the apex, subdepressed above and bellied or moderately convex beneath. When the egg is newly laid, its smooth,

semicoriaceous chorion is milky to pale yellowish white, but becomes medium brown with time. As the embryo advances toward maturity, the chorion becomes readily separable from the underlying thin white membrane, hence may remain as a lining of the egg pit when older eggs are dissected out of the hypanthium. This fact may lead to the false impression that the outer skin or layer is not a part of the egg, but a product of the injured hypanthium.

The caudal cap, or "brush," reminiscent of the cupule around the base of acorns, is fairly rigid, brown, with numerous small pointed bristle-like processes and a larger, central knob or tassel-like process on its subflattened outer surface; its ental side is concave, and cuplike, embracing the round basal end of the chorion, but extending farther down over the lateral, than over the broader top and bottom, sides. The cap is perhaps an ornamental, not an essential functional structure, and probably develops and becomes a part of the egg when the latter is still contained in the ovarian tube.

Larva. The following key embodies the principal structural features that serve to distinguish the three larval instars of *Rhagoletis basiola* as they occur in rose hips from Illinois to northeastern Minnesota.

1. Larvae usually 2.0 mm. or less in length; mouth hooks with a prominent medioventral tooth but with a dorsobasal lobe (Fig. 11); hypostomium slender, unarmed (Fig. 11a); no prothoracic respiratory "fans," but two obscure U-shaped to oval caudal respiratory slits on each posterior plate (Fig. 4a, b, c).....First instar.

1—Larvae usually 2.0 mm. or more in length; mouth hooks with a narrow or obscure preapical tooth (Figs. 12, 13); hypostomium shorter, with prominent stout ventral processes; food channels, i.e., lattice-like stomal sieves (Fig. 10), subhypostomia and parastomia present (Figs. 12, 13); also prothoracic respiratory "fans," and three spiracular slits on each posterior stigmatic plate (Figs. 5, 6, 7, 9).....2.

2. Larvae mostly 2.0 to 4.0 mm. long; mouth hooks with a slender, narrow preapical tooth (Fig. 10); slits of posterior stigmatic plates oval, about twice longer than their maximum width (Fig. 6)....Second instar.

2—Larvae mostly 4.0 to 7.0 or 8.0 mm. long, found either in or emerged from hips; mouth hooks with a broad, short, rounded preapical tooth (Fig. 13); slits of posterior stigmatic plate elongate, slender and 4 to 6 times longer than wide (Fig. 7).....Third instar.

Puparium. Newly formed puparia are dark ocherous, becoming pale stramineous in a few days as the cuticle dries. Thoroughly wetting the puparium restores the dark color. Form oval, somewhat depressed; length varies from 3.0 to 6.45 mm., the maximum width from 1.0 to 2.85 mm. The length and diameter in a large sample of puparia varied

ratiowise, from 1.83 to 1.0 in the shortest small individual, to 3.59 times longer than wide in the slenderest large one (Balduf, 1958).

Expansion of the wings. On the newly emerged flies, the inflated ptilinum is sometimes temporarily visible. The wings are then mere small sacks that reach caudad only to the base of the abdomen. They are soft and crumpled, and their lumina still contain more or less bodily fluid that presumably represents blood and constitutes the agent which effects expansion of the wings. The process of broadening and thinning of the wing sacks is first visible at the base, whence it spreads distad. In the intermediate stage of expansion, the wings are long and narrow, their front and hind edges parallel, and they lie well apart from one another and horizontal to the top of the body. In their final, fully developed state, the apices are broader and carried elevated at an acute angle to the length of the body, also in a transversely oblique position—the anal area adjacent to the abdomen, the costa at a higher level.

During the process of wing expansion, the flies cling to a vertical surface, head upward. The rate of expansion was observed to be slower on cool rainy days, as compared with bright warm spring days. Ordinarily, the fly engages in its characteristic movements within a few hours of its emergence from the puparium. Like other picture-winged flies, *Rhag. basiola* may stride grandiosely about while pirouetting the elevated colorful wings.

Time of emergence. In the course of attending the rearing cages in the earlier years of this investigation, I casually observed that the adults of *Rhag. basiola* seemed to emerge from their puparia only in the hours between dawn and noon of the same day. Scarcely prepared to believe that they issue only in one restricted period, day by day, I instituted a plan of checks in which the first inspection of the rearing cages was made at about 6:00 A.M., and, in many cases, at or before dawn, and thereafter as many times in the day as other duties permitted. The number of flies found in each cage was recorded at each inspection. The crop of flies in each cage was removed between 4:00 P.M. and midnight of each day. Extending this program of checks through the seasons of emergence of the years 1946, 1947 and 1948, it was established that *Rhag. basiola* indeed has a period of emergence each day that begins approximately at sunrise and terminates, with few exceptions, by 10:00 A.M., standard time, of the same day. This emergence pattern holds true for Eaglesnest, Minnesota as well as Urbana, Illinois; hence it is not merely a phenomenon induced by some peculiarities of local environment.

Data on these observations are presented in Table 1, and are based on 12 complete daily records taken in June 1946, 1947 and 1948, when

emergence from the overwintered puparia was at its numerical peak. The percental values show that emergence occurs largely between sunrise and noon, and that the time of inception and completion of the daywise emergence is influenced by temperatures, being delayed when the average readings Fahrenheit for the 10 hours preceding 6:00 A.M. varied between 51 and 59°, and occurred earlier and earlier in the morning as these average temperatures increased to 70 to 74°, in shade. Excepting one day of the 12, the morning hours averaged warmer than the predawn hours.

TABLE 1. PERIODIC EMERGENCE OF *Rhagoletis basiola*
(Selected days in June, 1946, 1947, 1948)

Average temperatures in 10 hours preceding 6:00 A.M.	Number of flies issued	Percentage of flies emerged			
		Prior to 8:00 A.M.	8:00 to 10:00 A.M.	10:00 to 12:00 noon	After 12:00 noon
51-59° F.	38	0	24	32	44
60-64	43	0	86	14	0
65-69	141	28	69	3	0
70-74	63	94	6	0	0

This periodicity apparently may be explained by the probability that the process of pupal development to the emergence-ready adult state is alternately retarded by the relatively cool temperatures of night and accelerated by the warmer daytime temperatures during May and June.

Let us choose several successive days out of the season in order to illustrate the nature of the alternation. Each daily yield represents a fraction of the total sample. On the first day, we find a number of pupae that have matured to the state of emergence, and these issue as flies during the daylight hours of the ensuing morning. In the total sample of pupae there is also a number of individuals so immature that they cannot quite develop to the state of emergence as adults in the remaining warm afternoon hours of the day. The further development of this number is retarded by the falling temperatures that usually characterize the ensuing night. Since night temperatures mostly reach the lowest point just before dawn, accelerated progress of this fraction toward the state of emergence must await the warmer sunlight hours of the new day. Thus accumulates a crop of subadult individuals from noon to dawn, due to the submaturity of the pupae and the retarding influence of cool night temperatures. This crop will emerge on the morning of the

second day. The individuals that constitute the daily fractions or crops of flies, have attained the emergence-ready state to various degrees, as a result of which their emergence is not simultaneous, but spread over the several hours of the forenoon.

To demonstrate a theory that irregular temperature is one of the factors causing this restriction of emergence to the daylight hours of the morning, three lots of puparia were subjected to a constant temperature of 80° F. and a water-saturated atmosphere, beginning June 6, 1947. The sample of puparia reared from *Rosa acicularis*, growing at the mouth of the Cascade river on Lake Superior, yielded 56 flies between June 8 and 24; those from *R. arkansana*, Madison, Wisconsin, yielded 55 flies, June 12 to 23, and a third lot from *R. carolina*, Kickapoo Park, Illinois, 84 flies, June 12 to 28.

The constant temperature disrupted the natural pattern of emergence somewhat, in that flies began, on some days, to issue before 6:00 A.M., and others appeared after 3:00 P.M. However, the majority of them still emerged between the hours of 6:00 and 10:00 A.M. Had the puparia been held under the above constant conditions for a much longer period, e.g., from mid-April, preceding the attainment of the emergence-ready state, the appearance of the flies might have been continuous, rather than periodic.

Dunning (1956) describes a diurnal rhythm in the emergence of *Pegomyia betae* (Curtis), Anthomyidae, Diptera, from the puparium. In its general aspects, at least, this rhythm resembles the periodic emergence of *Rhag. basiola* described above. From experiments designed to identify the initiators of this rhythm in *P. betae*, Dunning suggests the phenomenon may be "induced by the effect of temperature or light fluctuation at some time before the late pupal stage, or that it might be inborn in the species, and that it is further regulated by temperature variation at the time of emergence. Further work will be necessary before the suggested explanation can be shown to be valid or otherwise."

Behavior. The adults are inordinately secretive under natural conditions, hence are seen but infrequently in association with their obligatory host plants. Their presence is usually first indicated by the dark speckles made on the rose hips by the ovipositor. They remain out of sight on a clear day, and are then resting, or engaged in limited walking or flight, in the shaded recesses of the rose bushes or adjacent vegetative cover. The flies obviously dislike direct sunlight, and because of their preference for the obscurity of deep shade, an observer might easily assume that the flies are rare and that only a few individuals produce all the eggs found in local situations.

In my observations of this species, they came out to plain view in the cool shade of evening and during the daytime only when the sky was

heavily overcast. Even when the males, which were visible more often than the females, were abroad as if alert to find mates, they mostly confined themselves to the undersides of leaves and also the hips. Possibly because males are less sensitive to light, or are impelled by sex urge, they appeared somewhat less secretive than females. The females seem to be less aware of, or responsive to, light when preoccupied with oviposition, yet this function is discontinued when the sun breaks through the clouds for a few seconds.

Feeding. The flies which had been caged for observation of mating and oviposition fed readily on water solutions of sugar or honey with or without supplements of baker's yeast. They also drank the water droplets which condensed on the glass chimneys.

Preening. The captive flies also spent much time in brushing themselves with their legs. In doing so, the front legs briskly stroked the sometimes flickering proboscis and the head, including the eyes, whereas the hind legs preened the abdomen, the wings, the ovipositor after it was withdrawn from the hip following oviposition, and were also used to rub each other.

Copulation. Mating pairs are seen but rarely in nature. Within the confines of the cages, it was observed that the advances of the usually aggressive male are sometimes resented, as evidenced by the vigorous sidewise movements of the female. Once the union is effected, the pair becomes comparatively imperturbable although flight is possible for short distances during copulation. The accepted male stands quietly astride his mate, his fore tarsi resting near the base of the female wings, while the other four feet contact the wings, abdomen, or the support on which the pair stands. In the copulatory posture, the apex of the female abdomen appeared linked to the venter of the male terminal segment. While so united, the male sometimes elevates his abdomen, and thereby draws the invaginated terminal female segments, that form the ovipositor, out to their full length. This seems to mean that the very apex of the ovipositor is attached to the male. The pair of pointed chitinous claspers are then seen to have their flat side applied against the antero-lateral faces of the everted ovipositor. In a few instances, pairs were discovered *in copulo* on the first day of adult life where no food was provided. Seven other pairs were in their second to sixth days when first seen united, but these were not certainly the first matings.

The females of the seven pairs lived 21 to 33 days when fed as stated above, the males from 17 to 28 days, during the period, July 16 to August 21. Copulation by the seven pairs was seen to be repeated from four to 10 times in as many days. The unions generally occurred on successive days, but in some cases, at intervals of one to several days. The interrup-

tions appeared to be associated with temperatures in the sixties. The mating activities of all the pairs was most intense during the first half of the recorded periods of adult life, and particularly so in the first two to three days. In a specially noteworthy instance, a pair continued joined night and day for 33 consecutive hours. It seems certain in this case that the then low temperatures prolonged the union. Copulation is probably not initiated in such temperatures, but seems to persist so long as cool weather prevails following its inception. No mating was observed in the last 3 to 7 days of the life of six pairs. In the case of the longest-lived pairs, whose male died at age 28 days and the female at 33, copulation was not seen in the final 17 days.

Oviposition and egg. Data pertinent to the process of placing eggs into rose hips, and the development of the embryo, were obtained by the following means: (1) oviposition was observed both in the laboratory and the field; (2) approximately 30,000 hips were examined in the field in order to determine the percentages that bore ovipositional punctures, and dates of same; (3) samples of punctured hips, totaling about 3,000, were dissected microscopically to learn the manner of placement of the eggs and the gross development of the embryo.

The females that actually laid eggs under observation were about 12 days old. In general, in this procedure the fly settles upon a hip, and bends the apical part of the abdomen downward, sometimes obliquely backward, sometimes at an angle of about 90° with the base. Next the entire body, pivoting on the legs, rocks alternately and vigorously forward and backward for some seconds or longer. By this means, the awl-like terminal section of the ovipositor effects an oval puncture in the skin and a pit in the underlying flesh of the hypanthium. When the rocking ceases, the distal two segments of the drill have entered the hypanthium, while the end of the broader, blunt third segment rests against the skin of the hip.

Then the abdomen is lengthened and shortened alternately in a pulsating manner, and exerts backward thrusts for several minutes. In some cases, the proboscis flickered rapidly during the pulsating thrusts. In this phase, the egg probably passes from an oviduct, through the ovipositor, and into the egg pit. The fly then remains still for a minute or more before she withdraws the ovipositor from the pit. With captive flies, the work of drilling an egg pit and placing an egg into it was observed to require 12 to 24 minutes. The duration is probably determined by the hardness of the hypanthium more than any other factor.

The egg pit necessarily conforms closely to the length and form of the egg, being approximately 0.3 mm. in diameter and 1.0+ mm. in depth. Initially, the broadly oval aperture is not visible without careful search and magnification; but in less than a week, the marginal skin tissue of

the hypanthium, disrupted by the ovipositor, turns dark brown to black. Then the number of punctures can readily be counted without aid of a microscope. However, brown specks of a corky texture that probably represent a kind of plant disease, may sometimes be mistaken for egg punctures, until scrutinized with a microscope.

The outer or caudal end of the inserted egg sometimes protrudes slightly above the adjacent surface of the hypanthium so that the ornamental brushlike caudal cap remains visible externally; at the other extreme, the egg is often distinctly countersunk, as much as one-fifth its own length. The hypanthium sometimes swells convexly over and around the egg, a condition that appears associated with the hard texture of green, growing hips. Rarely a fly makes two pits through a single external puncture, the pits then forming an inverted V, but only one of the pits has contained an egg. Numerous dissections of hips (40 per cent of all recorded for *R. blanda* and 19 per cent for *R. acicularis*) leave no doubt that many pits are incomplete, and therefore contain no egg. The pits vary in depth, from mere shallow breaks in the skin to full depth, so far as one can judge. Old incomplete pits are filled with a hard conical brown plug formed of desiccated sap that oozes from the hypanthial tissue. Many careful examinations seem to indicate that the hardness of the hypanthium is the principal cause of incomplete pits, since they are found largely on hips that have grown to full size yet remain green and so flinty hard that small pieces may be chipped off with a scalpel. However, in some cases, absence of eggs from apparently complete pits may signify interruption of the ovipositing fly by natural causes, e.g., leaves of the plant blown against her by the wind. It is also reasonable that the fly may become so tired from boring into hard hypanthium that she desists before an egg can be inserted.

The positions taken by the fly when she implants the eggs may be learned from observing her in action, and also from the angles at which the eggs lie in the dissected hypanthium. The longitudinal axis of the fly more or less closely parallels the long axis of the hip, with the fly's head directed toward the floral end as she clings to the lower, shaded and comparatively green ventral side of the hip. Rough diagrams made during dissection of the rose hips, to indicate the position of the eggs in the hypanthium, show that most eggs were set at various slants or angles, rather than vertically. The angles ranged from vertical to subparallel with the surface at the point of insertion, i.e., 15 to 90°, with the majority lying at intermediate angles of 35 to 85°.

Both the sketches and direct observations showed that all but a few eggs are placed into the basal half of the hip and into its green underside. Of 810 punctures recorded from *R. blanda*, 92 per cent occurred on the petiolar or basal half, 7 per cent on the transverse or equatorial

line, and 1 per cent on the apical half. For *R. acicularis*, the number on the free or distal half was somewhat larger. Only rarely were eggs inserted into the lateral faces or the sun-reddened upper sides. This predominance of eggs or incomplete pits on the basal and ventral areas seems to result from two factors—one environmental, the other inherent in the behavioral characteristics of the fly. As to the first, the sepals of the calyces largely lie recurved over the floral or distal part of the growing hip, thus affording a rough and effective support for the fore legs of the fly during oviposition, and, at the same time, they prevent the insertion of the ovipositor into this same distal area of the hip. Second, the pronounced negative phototropism of the fly appears to explain the strong preference for the underside of the hip as the place for oviposition. The predilection for the basal half favors the larvae since the hypanthium is thicker, bulkier here, affording them more food and living space. However, this same preference is a handicap because the area ripens and mellows later than the sunned upper surface. This circumstance tends to retard or thwart the feeding and burrowing of the first instar until it reaches the more penetrable, riper parts of the hypanthium.

Rhag. basiola never inserts more than one egg into a single pit, although two or more deposited eggs per hip are not unusual. In such cases, differences in the age of the embryos show the several eggs are not laid in close succession by a single fly. In no instance was an egg found in the central or achene cavity of the hip. Limitation of the egg to the hypanthium may be explained by the observations that the majority of the eggs are placed in the thick basal part of the hip wall, and most of them lie more or less obliquely in it. Normally, the capless cephalic end of the egg is first to enter the pit, with the result that the larva, upon hatching, enters directly into the flesh of the hypanthium which constitutes its food. Six of the hundreds of eggs found *in situ* appear to have been inserted caudal end first, for the dark brown mouth hooks of the advanced embryos were visible in the outer end of the pit. Thus, the brown, brushlike cap, which normally embraces the cauda of the egg, lay over the cephalic end. Where such inverted embryos lie considerably countersunk in the hypanthium, the hatching larva may possibly bore into the hip directly from the upper end of the egg pit.

Oviposition and rose hosts. The number of pits and eggs differed noticeably with reference to the hips of *R. acicularis* and *R. blanda* investigated at Eaglesnest from 1945 to 1950. Of the 6,652 hips of *acicularis* examined 907 bore 1,094 pits, or an average of 1.21 per hip, whereas 1,239 of 19,305 hips of *blanda*, including *R. Macounii*, had 2,084 punctures, or an average of 1.69 per hip. However, the percentage of eggs in the pits was higher in *acicularis*. Eggs had been laid into 81 per cent

of the pits in *acicularis*, whereas only 60 per cent of the pits in *blanda* contained eggs. The hips of *acicularis* not only develop and ripen earlier in the over-all ovipositional period, but are generally more penetrable to the ovipositor and the resulting larvae, as compared with the later-ripening, harder hips of *blanda*. Although the hips of *blanda* mellow later in the season and the fly then achieves a greater success than earlier, the over-all advantages in *acicularis* are more favorable to success. The differences in texture and ripening time of the hips of these rose species go far toward explaining the larger population of *Rhag. basiola* in *acicularis*.

Embryo. As the embryo develops, the chorion changes from the pale yellowish white of the newly laid egg to pale brown, a change in color possibly effected by the stain of fluid released from the cells of the hypanthium ruptured by the ovipositor. Recently laid eggs remain free within the pit walls and are readily removed intact by chipping bits of the contiguous tissue away with a fine scalpel. The chorion later becomes fused to the wall of the pit, probably by the cell sap that dries around it. As the advanced phase of the embryo is reached, the chorion separates from the inner membrane, and the more or less mature embryo can be worked out with probes, leaving the chorion as a lining in the egg pit. These conditions facilitate gross identification of successive phases of the developing embryo.

Three quickly identifiable phases of embryonic growth are recognized: early, intermediate, and advanced. The first is indicated by the pale freshness and plump form of the chorion, the granular texture and stringy consistency of the grayish white yolk, that seems to signify an incipient and grossly amorphous embryo. The intermediate phase is characterized by its definite larva-like form, still straight tubular alimentary canal and the absence of bodily segments and mouth hooks. The advanced phase is recognizable at a glance by its over-all resemblance to the first instar of the larva, i.e., by the well-developed segmentation, the reddish to dark mouth hooks and the convoluted alimentary canal clearly visible in the caudal half of the abdomen. Casual observations indicate that the first two phases are of short duration, but the third persists through more than half of the embryonic period.

Deficient eggs. A small percentage of the eggs found in rose hips had chorions of normal color, size and form, but were subnormal in that they contained only a fluid having the color and consistency of cow's milk. I have considered two theories to explain this condition. First, it may result from failure of fertilization. But this cannot be the cause, since the normal, grayish white, granular yolk forms in the ovarian tubules independently of the sperm. Second, it may signify a deficiency in

nutritive materials such as may characterize old, reproductively exhausted flies.

Also observed repeatedly in egg pits, in the absence of larval burrows, were dry, collapsed chorions of dull color. These appeared to be empty, or, at least, they contained no macroscopically recognizable solids. This condition suggests that these are deficient eggs from which the milky fluid evaporated in the course of the summer. This belief is strengthened by the fact that collapsed empty chorions were found from late July into September, i.e., in the later part of the reproductive season, when adequate time for desiccation had elapsed. It therefore appears probable that the milky state of the egg antedates the dry collapsed condition of the chorion.

Larval habits. It may be taken as a fact that the embryo, when developed to the state of hatching, uses its mouth hooks as a mechanism for escape from the enveloping chorion. All but a few of the embryos lie headed toward the inner end of the egg pit; hence, as hatching larvae, they issue directly into the substance of the hypanthium.

The rate of progress in burrowing, and also of growth, of the first instar is definitely influenced by the condition of the hypanthium. Many rose hips are hard when immature and green, and the degree of hardness in this stage of their development varies from species to species. For example, those of *Rosa blanda* are then flinty in texture, as compared with the inherently less firm hips of *R. acicularis*. One of the impressive facts learned in dissection of the hips of *blanda* was that the first instars of *Rhag. basiola* suffer a high rate of mortality. Many of their burrows were incipient to short, with thickly encrusted rough brown walls. The dead, blackened shrunken larva was then found at the fresher end of the burrow. This frequently observed effect obviously resulted from the inability of the larva to ingest any of the hypanthial tissue, or enough of it to survive. Later in the season, August to September, the hypanthium of *R. blanda* mellowed and ripened, and only a few newly dead first instars were then found.

When the hypanthium is sufficiently soft, the larva rasps a simple subcylindrical burrow, which gradually but slightly enlarges in diameter as the insect doubles in thickness in the course of growth from hatching to the first molt. As the larva advances through the hypanthium, the walls of the older sectors of the burrow become encrusted, particularly when the hypanthium is unripe and juicy. The crusty layer probably results from solidification of juices that ooze from the cells disrupted by the larval mouth hooks, forming a rough brown surface and reducing the diameter of the burrow. But encrustation is less in extent, or lacking, later in the summer when the hypanthium softens and ripens, particularly in *R. acicularis*.

The burrows of the first instars occur at various depths and areas of the hypanthium. In hard unripe hips, they may pass just under the skin of the hypanthium, and, being encrusted and dark, their straight or winding paths may be traced externally. Other burrows extend along the floor of the hypanthium, adjacent to the achene cavity, but do not penetrate it. The majority pass through the fleshy middle level. While 90 per cent and more of the eggs of *Rhag. basiola* are inserted into the shaded green underside of the basal half of the hip, and most burrows are therefore initiated in this area, the larvae do not limit themselves to it. Many of the first and second instars were found to inhabit the thick basal part of the hypanthium, and the petiole was circled by some of them. Others proceeded toward or to the floral half, where they not infrequently ringed the necklike constriction at the base of the calyx. Again, some larvae invaded the mid or equatorial area of the hip, including both the green underside and the reddening or ripe sunned surface, while others bored lengthwise in a straight or sinuous line from base to apex.

Despite these variations in location, depth and direction of the burrows, I hold that the burrowing is not wholly fortuitous. Assuming the behavior of the larva to be made up of a succession of reflex responses, it seems probable that the textural, chemical and nutritional properties of the hypanthium, the orientation of the hip on the plant and the position or posture of the eggs in the hypanthium, determine the pattern of the burrows and that the boring behavior may be fundamentally uniform.

The maturing larvae, and especially the third instars, due to their greater bulk and feeding capacity, and also the concurrence of softening ripe hypanthium, are not limited to the cylindrical type of burrow. Instead, by increasing the width of the burrows and by creating branches, cavities of greater or lesser size are produced that may be described as blotch mines. The larvae lie in the margins of these mines, in contact with the living tissue and removed from their excrement (which resembles apple butter in appearance and consistency) in the area previously occupied. The mine may involve a quarter or more of the entire hypanthium, depending on the size of the hip and the larva; or several mines, representing a number of larvae in a hip, may involve almost all of the hypanthium. Rarely was any one hip found to harbor simultaneously more than a single third instar but hips, particularly of *R. acicularis*, were commonly inhabited also by two or three earlier instars. In the latter cases, the slender tunnels of the small individuals may be disrupted, and the larvae themselves incommoded, by competition with the large larva for food and space.

The hypanthium overlying the undermined sectors turns dark, and

when the ripe mushy tissue is rasped off cleanly, the skin proves to be whitish and transparent, or window-like. The hips so infested also lose their plump convex form as the skin collapses into the mines.

The mature larvae of the fly emerge head first by making local, irregular breaks in the skin at various parts of the hypanthium above their blotches, from petiole to distal half. The flaps of the skin involved in the exit hole may resume their natural position after the larva has wormed out. The discovery of the holes as evidence of emergence therefore may require close inspection of the inhabited hip.

Larval population. The number of *Rhag. basiola* larvae present in any one time, place or rose host is most conveniently ascertained by collecting the mature larvae as they normally issue from hips in late summer and fall. The data pertaining to larval populations reported below were secured by storing more or less ripened hips in fruit jars, and removing the emerged larvae or puparia, usually at daily intervals. In the years 1944 to 1950, approximately 70,000 hips were under observation, and 9,752 mature larvae or puparia of this species were obtained. Assuming one individual per hip, 14 per cent of the hips contained a larva. The error due to the occasional presence of two, or rarely three, larvae per hip is probably more than counterbalanced by another error due, in some samples, to the emergence of the earliest fraction of the larvae while the hips still hung on the bushes in nature.

Sixty-five separate samples compose the over-all lot of hips observed. The component lots vary from 20 to 5,835 hips representing 10 species of roses: *R. acicularis*, *blanda*, *Macounii*, *arkansana*, *palustris*, *canina*, *virginiana*, *eglantaria*, and *woodsii*.

The tentatively tabulated data derived from the above rearings showed first a striking range in number of larvae per unit number of hips. The most impressive aspect of this percentile variation is the somewhat steady decline in the ratio of larvae to hips from the northern to the southern limits of the range. A series of examples representing the successively lower latitudes shows this feature clearly. At Ely and the nearby vicinity of Eaglesnest Lakes in northeastern Minnesota, 54 per cent of the 5,500 hips of *R. acicularis* processed from 1944 to 1950 yielded mature larvae of *Rhag. basiola*. Similarly, 40 per cent of 5,104 hips of *R. blanda* from the same years and part of Minnesota, produced larvae. Farther south, in extreme northwestern Wisconsin, 2,276 hips of *R. blanda* proved to be inhabited at the average rate of only 7 per cent over a three-year period.

At Chetek and Rice Lake, Wisconsin, 17,751 hips from *R. blanda* and *R. carolina* contained larvae at the rate of 9 per cent. And finally, from northern to central Illinois, so far as Ridgefarm below Danville, and Taylorville, 16,340 hips of *R. carolina* yielded 682 larvae, or a percent-

age of only 4. Some large samples taken in the Illinois area were entirely without the species. Below latitude 35°, *Rhag. basiola* has not, to my knowledge, been reported.

In addition to this variation in the north-south direction, secondary differences occur locally, that may be correlated with varying suitability of the several rose hosts, conditions of drought that shrink the hips and render them intolerable to the developing larvae, severity of the winter seasons, and certainly, as will be shown below, the numerical fluctuations of several endoparasites of the larvae and puparia. Therefore, larval populations of *Rhag. basiola* are locally, as well as geographically, subject to much quantitative variation.

Pupariation. In September and October, at Urbana, the mature larva of *Rhag. basiola* undergoes the change to the puparial form within the day it emerges from the rose hip. In its natural habitat, its several hours of prepupal mobility doubtlessly are spent in establishing itself in the duff or soil under the rose plant. When contained within a glass vessel, this larva crawls about energetically for an hour or more, then gradually reduces its rate of travel until the inevitable process of pupariation completely immobilizes it. Larvae that emerge in the cool later part of fall required as much as 10 hours to transform and, at near-freezing point, a few failed to pupariate. During the change from larva to puparium, the body shortens, thickens and becomes oval, and the soft white cuticle becomes leathery, then hard and ocherous yellow. If kept in dry atmosphere for several days, the puparium loses a considerable amount of weight and its cuticle turns brittle and pale stramineous, but if then placed on water-soaked cotton, it regains its lost weight, leathery flexibility and ocherous color (Balduf, 1957).

Commonly the puparia became so firmly attached to the surfaces of the glass containers in which they had transformed that their shells sometimes broke, with fatal consequences, when they were pried loose. At first I supposed that the adhesion resulted from the sticky hip juices through which the larvae had crawled. But according to Fraenkel and Brookes (1953), who observed similar attachment in other higher Diptera, the almost fully contracted larvae suddenly pour forth a clear liquid from their then enlarged salivary glands. This secretion spreads over the venter of the body, hardens quickly and serves to cement it to the support. Possibly this is the mechanism of attachment also in *Rhag. basiola*.

Prepupa. For three to five days of normal fall temperatures at Urbana, the newly formed puparium contains a body which, in this form or stage of dipterous insect, has sometimes been regarded as a fourth larval instar, and in which it still resembles a larva both in external and internal

organization. Within a few days it becomes transformed into a pupa, with marked structural and physiological changes. This process suggests that the hypothetical fourth instar is not larval. As a substage of Diptera, it is homologous with that occurring just before the pupal stage of other holometabolous insects, where it is recognized as a prepupa. In *Rhag. basiola*, this stage begins with pupariation and terminates with the exuviation of the prepupal cuticle and the externalization of the leg cases and wing pads and the division of the body into three distinct regions.

A casual examination of the viscera of a prepupa one to three days old reveals its more obvious structural features. Most prominent is the extensive bulky fat body. As in the larval instars, this consists of a thin network composed of numerous minute clusters of "fat" cells, each of the clusters consisting in turn of many still smaller cells and linked to other clusters by short threads. The network conforms to the shape of the body cavity and the visceral organs for which it forms a lining. The web disintegrates into its numerous separate component clusters when the insect attains the early state or phase of the pupa, i.e., about the third to fifth day following the inception of pupariation. The alimentary canal retains its larval form but is now empty, transparent and therefore obscure amid the massive fat clusters that envelop it and all other organs in the body cavity. Only the fusiform sector of the mid intestine, that lies just anterior to the Malpighian tubes, remains readily visible due to its content of an elongate slender spindle-shaped reddish brown solid mass of feces-like substance. Another system of organs easily distinguished amid the voluminous fat body is the pair of yellow, or sometimes greenish yellow, Malpighian tubes. One tube arises from each lateral side of the alimentary canal at the juncture of the mid and hind intestines. Each consists of a short basal stem, which bears two long, filiform, flexible chainlike arms of equal length. On close inspection, the pair of whitish, wiener-shaped salivary glands, supported by their short slender ducts, can be seen. But the status of the muscles, heart, nerves and tracheae cannot be ascertained by casual examination, and presumably will be generated from the imaginal disks during the later phase of pupation.

Gas in prepupae. The abdomen of the prepupa of *Rhag. basiola* was regularly found to be inflated with a quantity of clear gas. It may be seen in the body removed intact from the puparium, or, in some cases, through the puparial wall. On account of their inflated state, the prepupae are so reduced in weight vs. bulk that they float lightly on water. Reference to my numerous notes on this phenomenon shows that the gas is present during September and October, and specifically in puparia containing prepupae aged one to four days but mostly about three days,

but not in the subsequent early phase of the true pupa. Small, weak prepupae lacked the gas, whereas prepupae parasitized by first instars of the chalcid *Halticoptera rosae* Burks contained moderate amounts of it. Since the gas represents inspired air and occupies the body cavity of the prepupa, it seems likely that it incidentally provides the supply of oxygen for the parasitic larva. It also appears likely that the pressure exerted against the inner wall of the prepupal body cavity may aid the eversion of the pupal appendages, which marks the termination of the prepupal stage.

The gas was found to vary in amount from little to so much that it occupied most of the lumen of the abdomen. The amounts may possibly be correlated with parasitism and ordinarily the age of the prepupa, the older individuals possibly having consumed larger quantities of it in respiration. Snodgrass (1924, p. 25) states concerning *Rhag. pomonella* Walsh that "this gas is evidently the respiratory medium of the pupa," and that it gains entrance through the anterior tracheal tubes.

Pupation. At Urbana, the prepupa transforms to the true pupa in three to five days after pupariation. This takes place primarily in September and October. In this study, the newly formed pupa is designated the "early phase pupa," but in more formal terms it has been called, by Snodgrass (1924) and other investigators quoted by him, the "cryptocephalic substage" of the pupa. Its salivary glands, Malpighian tubes, and the alimentary tract with its small red-brown mass of waste, remain identical with those of the prepupa. The prepupal skin, having been molted at the termination of the prepupal stage, is retained unbroken around the pupa and forms a lining to the puparial wall. The three distinct body regions are evident, as are also the evaginated wing pads and leg sacks. These appendages appear as empty chitinous shells except that their lumina contain a few, free-floating particles of fat body. Particularly the leg sacks become obviously longer after the inception of pupation, and their extension backward to the apex of the abdomen is an easily identified indication that the early phase of the pupa has been attained. Insofar as gross observation can determine, all normal individuals of this species uniformly attain precisely this structural or developmental early pupal state during August to late fall, and, moreover, appear to undergo no further changes, either externally or internally, until the following spring.

Pupal diapause. This early phase pupa exists in a state of suspended development or diapause of eight or nine months over the fall, winter and spring seasons. The small early fraction of the mature larval population attains this condition in late August, the rest in September and October and even as late as early December, as in the case of larvae obtained

at Kickapoo Park in 1946. Were it unfavorably low atmospheric temperatures that induce the diapause, the larvae maturing in the warm weather of late August or early September would have advanced farther toward, if not to, the adult stage than those emerging from the hips from late September to late October, or thereafter, when cooler to cold weather prevails. Instead of wintering as prepupae, pupae in different phases of development, or as adults, the species uniformly, and regardless of the season or temperature, attains one developmental stage only, that of the early phase pupa, before winter sets in. This invariable confinement of the winter stage within these narrow structural limits implies a causative factor of an equally constant character which is independent of environmental temperature.

Heart beats of pupa. From the dorsal aspect, the beating heart of three early phase pupae was observed. The observations were possible when pupae were extracted unbroken from the puparia, or as breaks in the dorsal puparial walls afforded a view of the pupae within. The pressure of the air bubble in the pupae caused the meshes of the adipose web to spread, and the pulsations of the underlying heart alternately enlarged and diminished the aperture, so that the number of beats per minute was readily counted.

The rate of the beat in two pupae was 85 and 100 per minute. In the first there was a slight pause about every three or four beats which indicated an occasional prolonged dilation, as if pulsations were about to stop, but the pause was followed by a quick contraction. In the third pupa the beats occurred at the rate of 90 in one sample minute, and increased to 125 after approximately 15 minutes of exposure to warmth from the microscope lamp. When this pupa had cooled about 15 minutes, the pulsations had decreased to 120 per minute.

Spring development of pupa. When the puparia, kept on soil in flower pot cages during the winter outside, are brought in, in early May, they contain pupae which have remained in the early phase they had attained in the previous fall. The disintegrated adipose material still fills the body cavity, and the salivary, digestive and excretory organs retain their winter condition. Pupal development is resumed between the third week of May and early June. A perceptible change takes place in the texture of the fat particles. These are now further disintegrated, the clusters being resolved into their much smaller component granules, giving the fat substance a smooth, homogenized, creamy appearance. Gradually this mass of material is consumed, being apparently utilized for the formation of the organic systems of the adult insect from the imaginal discs. For example, the tarsal cuticles which, in the early pupal phase, evidenced segmentation only as shallow, broadly rounded con-

strictions, now contain the developing segments of the adult tarsus within. At first vague and devoid of vestiture, but gradually more distinct and spiny, the tarsal segments serve as a readily observable measure of the progress of the pupa toward the mature adult state. Simultaneous with the development of the tarsi, the well-formed head, antennae and mouthparts, the reddening eyes and their concise facets, the advent of the dark bristles against the background of yellow and orange body regions, and the appearance of veins in the immature wings were further indications that the fly would soon employ its ptilinum to effect escape from the puparium.

However, not a few puparia yield no flies, or yield them belatedly. Parasitism by the larvae of *Opicus* and *Halticoptera* permits the host to pupariate but destroys it before the pupal stage is attained, or completed, respectively. Undernourishment due to competition with other larvae of their own species, or those of *Cydia packardi* in the same hip, or the chance that they may inhabit dry, diseased or overripe hips, may result in larvae so weak and puny that they can barely pupariate, but develop no farther.

Prolonged pupal diapause. Of special interest were nine normal puparia which failed to yield adults in due season. When these were discovered, they had persisted three to six months beyond June to July, the months in which adults normally emerge. They had originated from hips of four different species of roses in Minnesota, Utah and Nebraska. However, they had two features in common: all were among the largest and most vigorous of their lots, and the eight which I dissected contained large healthy pupae, still in the early developmental wintering phase. So far as treatment is concerned, the nine puparia suffered various degrees of desiccation due to my neglect for three months or more. I wetted the ninth puparium with water, suspecting it to be in a state like that of the eight. This puparium then yielded a large normal fly, but a full year after the usual June date. It puparated in the fall of 1947, therefore should normally have become an adult in June of 1948, but, presumably because it had suffered desiccation, issued as an adult in June, 1949.

Perhaps the vigor of these pupae, or the character of the puparial walls, enabled them to tolerate the partial desiccation, whereas individuals of less vitality might have perished. Presumably the eight would have produced flies in the manner of the ninth, had they been spared and wetted. These instances of delay exemplify a form of development which differs from that characteristic of all early phase pupae of *Rhag. basiola* only in that it persisted a year longer. Such cases warrant further study with reference to the causative factors.

Life cycle. All the pertinent data obtained show that *Rhag. basiola*

completes one entire cycle, or generation, in a year in all the states and provinces from which materials were obtained. These data were derived from cage rearings of hundreds of adults, from emergence records for more than 5,000 mature larvae from hips, dissection of more than 700 hips from the field to determine the season of embryonic and larval development, and from examination of puparia of all ages to learn the winter state and subsequent progress of pupation. Acquired primarily in the years 1945 to 1950, the records pertain chiefly to northeastern Minnesota, northwestern Wisconsin and east central Illinois.

Adult life begins with the emergence of the flies from the overwintered puparia, which was continuous at Urbana from May 17 to July 12, an over-all period of 56 days. Year by year, the inclusive periods of emergence were 1946: May 30, July 3, or 35 days; 1947: May 17, July 10, or 54 days; 1948: May 28, July 6, or 40 days; 1950: May 30, June 27, or 29 days. When fed on an aqueous solution of sugar or yeast, females lived 21 to 33 days, males 17 to 28 days.

Allowing a preovipositional period of 12 days, egg-laying may begin at Urbana before June 1; however, egg pits were first found on *R. palustris* on July 4, 1949. The number of punctured hips increased rapidly to 90+ per cent by August 16. Possibly the latest occurrence of ovipositing flies in the field (at Eaglesnest) was September 3 to 4, as indicated by the discovery of newly laid eggs in hips.

The embryonic period involves at least the months of July and August. Five-year records for Eaglesnest show that only embryos, i.e., no larvae, occurred on July 10 to 12 in hips of *R. acicularis*. Some embryos remained in the field samples of hips from August 23 to September 1, indicating that oviposition may continue well into September. The duration of embryonic development may be estimated by dissecting eggs of known age and by observing first dates of oviposition and newly hatched first instars. At 11 days, the embryo had already reached the advanced phase, as indicated by its maggot-like form, convoluted alimentary tract and fully developed mouth hooks. Embryos 17, 23 and 24 days old had made no macroscopically observable advance over that seen in the 11-day embryo. The first egg was laid on *R. palustris*, Urbana, on July 4, 1949, and the earliest first instar was discovered August 11, or 38 days later.

These evidences indicate that embryonic life may be as long as five weeks or more, and that the early and intermediate phases are completed probably in much less than 11 days. The unusual duration of the advanced state suggests that a limited diapause is involved. That this phase is comparatively long is shown also by the fact that by far the most embryos found through several summers at Eaglesnest were in this state.

Larval stages, as well as other stages, are influenced by the prevailing

temperatures. Some first instars had hatched on August 11 at Urbana, but these were probably not the first, considering that small first instars were found July 17 to 19 in a five-year study in relatively colder northeastern Minnesota. Some first instars persisted at Eaglesnest to September 1, and the comparatively large numbers showed that they may extend far into this month. Second instars were found from August 18 to September 1, while third-stage larvae also occurred during all that time. Clearly, second instars continue far into September, and rearing records prove conclusively that the third instars mature and emerge from the hips at Eaglesnest from August 22 to October 15. At Chetek, Wisconsin, the mature larvae emerge from near September first to October 24. In east central Illinois, emergence begins about mid-September, commonly continues into early November, and in the instance of one sample from Kickapoo Park, larvae issued to December 13, 1945. Thus, the emergence of mature larvae from hips appears to occur later from north to south, or from the colder latitude in northeastern Minnesota to the warmer in central Illinois.

The time required for the development of individual larvae may be estimated or approximated from the dates of the earliest first instar and the dates the first mature larvae appear from the hip. Such data, obtained from *Rosa acicularis* and *R. blanda* at Eaglesnest in five years, indicate that the individual larval development required 30 to 35 days.

Since pupariation occurs within a few hours after the mature larvae leave the hips, and the early phase of the pupal state is attained in 3 to 5 days in average temperatures, the time period of this early pupa begins only half a week after the dates of larval maturity, i.e., from mid-August to early December, but usually late October, and persists through the winter into mid-May or June of the ensuing year. In May to June, pupal development resumes and continues into July. The emergence of the adults from the puparia—between May 17 and July 12—marks the termination of the pupal stage which may extend from mid-August of one year to July of the second year. The adult flies, after a preovipositional period of about 12 days, initiate the next annual cycle when the females introduce their eggs into new rose hips.

Under average conditions, the yearly development proceeds approximately as follows in the over-all area involved. The larvae in the hips mature and emerge, and pupariate within a few hours, from late August to late October. In three to five days the larva undergoes transformation through the prepupa to the early or cryptocephalic phase of the pupal stage which is then followed by a diapause lasting through fall, winter, and spring to late April or early May. Pupal development resumes in May, and adults issue from the puparia during a period beginning late in May and ending early in July. The flies oviposit into the hips from June

to early September, and the larva completes its three stadia from late July or early August to October.

HYMENOPTEROUS PARASITES OF *Rhagoletis basiola*

I have found four species of parasitic Hymenoptera that attack the immature stages of *Rhagoletis basiola*. Three of these have been identified as new; two species of *Opius*, Braconidae, and one of the chalcid genus, *Halticoptera*, Pteromalidae. The identity of the fourth remains in doubt, owing to its scarcity and my fruitless efforts to rear the adult. Some evidences, to be stated later, indicate that it may be a chalcid of the family Eupelmidae.

All these parasites are solitary and internal, and, with the possible exception of the supposed eupelmid, have one generation in a year in coordination with the single annual cycle of the host.

Opius rosicola Mues. and *Opius baldufi* Mues., Braconidae, Hymenoptera

Hosts and distribution. These new species were named and described by Muesebeck (1949). *Rhag. basiola* is their only host known to date. The specific characteristics of hips from six species of *Rosa* (*R. acicularis*, *blanda*, *carolina*, *arkansana*, *virginiana* and *setigera*, and some varieties of the foregoing) appear not to affect observably the utilization of *Rhag. basiola* as a host. In general, it may be said that the parasites have been obtained from all species of *Rosa* for which adequate samples of hips, well-inhabited by *Rhag. basiola*, have been available for investigation. One notable exception was *Rosa Macounii* from Crete, Nebraska, whose hips yielded 146 flies but no parasites.

Opius rosicola was reared from puparia of *Rhag. basiola* that originated at Saskatoon, Saskatchewan; Eaglesnest, Ely, and along the Minnesota-U.S. Highway 61, in northeastern Minnesota; and at Solon Springs, Sarona, Chetek and Madison, Wisconsin.

Opius baldufi emerged from puparia of *Rhag. basiola* deriving from three points in Alaska (milepost 326 at Richardson highway, Fairbanks; milepost 297.3 Richardson highway at Big Delta, and 144 miles north of the Canadian border on the Alcan highway); from Eaglesnest, Ely, and the intersection of the Minnesota-U.S. highway 61 with Pike Lake Road, and at Bally Creek, near Grand Marais, Minnesota; and from Chetek, Wisconsin; Orono, Maine; Urbana, Illinois, and Kickapoo State Park, near Urbana.

The above records indicate that both species are widely distributed in North America, but apparently limited to areas northward from the

latitude of central Illinois, which appears also to be the range of *Rhag. basiola*.

Recognition of Opius spp. While the adults of these species of *Opius* are structurally very distinct, distinguishing bodily characteristics of the larvae were not readily observable and the matter was not pursued. No specific differences in modes of life have been observed, and for this reason the bionomics of the two species are treated simultaneously.

The following distinctive characteristics that mark the adults of *O. rosicola* and *O. baldufi* are chosen from the original descriptions by Muesebeck (1949). Most distinctive are the wing characteristics: compare Figures 14 and 15. Some of the data on the number of antennal segments are based on specimens in my collection.

Opius rosicola (Fig. 14). Head ferruginous; mesoscutum with a long, slitlike median impression on posterior half; first tergite of abdomen rugulose, with two dorsal keels converging to about the apical third, where they are obsolescent; stigma short, broad; antennae of females with 35 to 42 segments, males 31 to 42 and for the species as a whole, usually 36 to 38.

Opius baldufi (Fig. 15; wings). Head black, only the lower parts ferruginous; mesoscutum with a median dimple-like impression before hind margin; first tergite of abdomen rugulose, with two nearly parallel, widely separated keels on basal half; stigma long and narrow; antennae of females with 40 to 47 segments, males 40 to 47 and for the species as a whole, usually 44 to 47.

Both sexes of *O. baldufi* and *rosicola* have small inequalities in the number of segments composing the right and left antennae.

Sex ratio. In the years 1945 to 1951, at least 300 adults of *O. rosicola* and 100 *O. baldufi* were reared. The series of *rosicola* comprised 136 males and 153 females, and of *baldufi*, 42 and 48 respectively. These small samples indicate the probability of a 50-50 ratio of males and females in both species.

Adult and egg. In the field, the brown adults (Fig. 14) were infrequently seen resting on the leaves of roses or plants adjacent, as they flew somewhat briskly from place to place, usually for short distances.

The eggs (Fig. 16) of these *Opius* species, obtained by dissecting larval *Rhag. basiola*, are about 0.5 mm. long, with a broadly rounded, large cephalic end and a much narrower tapering caudal end. The chorion appears smooth, whitish and translucent. The large quadrate head of the advanced embryo is visible externally.

The activity of oviposition was observed only once in the field. When discovered, the female had already inserted the terebra deeply into a hip of *Rosa acicularis*, and lay quiet with the venter of her body fully

in contact with the upper surface of the hip. That an egg had been deposited was shown by subsequent dissection of the hip, revealing a first instar larva of *Rhag. basiola*, which, in turn, contained a newly hatched larva of *Opium* that had not yet ingested food.

The eggs found invariably remained free and unattached in the body cavity of the host. While eggs were not infrequently found in the host larvae, few of them contained living embryos; their scarcity indicated a brief embryonic life, probably one or two days. The majority of eggs present in the hosts contained no identifiable embryos but only dull grayish white homogeneous granules, apparently yolk. The frequency of such eggs leads me to conclude they were dead, probably unfertilized. The chorions of some such dead eggs had collapsed to various extents and had even become twisted or curled, and usually more or less brown. For convenience, I refer below to the latter as "brown bodies." These occurred in living second and third instars of the host, but mostly in puparia. Thus deformation and discoloration of the dead egg developed over a period of weeks in some instances, since the female attacks first instars as well as seconds and thirds.

The best evidence as to the host stages attacked by the ovipositing *Opium* are my records of early phase first instars found in hosts dissected. The retention of all or much of the gelatinous envelope around the body, and the simple thysanuroid form of the parasite are reliable indicators of such early phase larvae. Twenty-five such larvae were found in host larvae: 5 in first instars, 14 in second instars, 6 in third instars. The puparia of *Rhag. basiola* never contained parasites of this early phase.

First larval instar. The number of instars has not been ascertained but gross external structural characteristics indicate there are at least three. As in other opine Ichneumonidae, the first instars of the present species differ sharply in form from the subsequent ones (Clausen, 1940, p. 48).

The newly hatched first instar of *O. rosicola* and *O. baldufi* in its usually moderately curved resting form, is 0.6 to 0.7 mm. long, and enlarges to 1.5 mm. during its slow development to the molting state. The prothorax at first is barely as broad as the head, while the abdomen tapers behind, effecting an over-all thysanuroid form. Gradually the thorax and abdomen expand in all directions to the shape of a broadly round sack (Fig. 17), while the head retains essentially its original size and form. In this advanced phase of the first instar, the postcephalic region of the body remains relatively depressed but is twice as broad and thick as the head.

The head is quadrate, pale brown, and sclerotized, with a pair of median denticles on the anterior edge of the labrum; antennae are short, and appear soft and flexible; the mandibles are brown, prominent, and robust, falcate in form, attached under the protruding labrum, and may

be opened very widely; two obscure fleshy mamma-like extensible appendages arise from the sternum of the prothorax, one near each outer edge; the apex of each appendage bears a pair of obscure divergent spines. Being concolorous with the body and contractile, the "mammae" are usually not visible, but become briefly so when extended as the larva rolls over sidewise, or writhes energetically in a drop of water. The postcephalic part of the body consists of 13 segments, the small terminal segment being obscured by invagination in some postures. A broad-based minute spur is present on the mid-dorsal line of each of segments 6 to 9. The sternum of at least the first nine postcephalic segments bears a pair of minute bristles. The abdomen terminates as a pair of soft, transparent, extensible pointed processes, which appear joined to the thirteenth segment.

Some investigators (Cameron, 1941; see also Clausen, 1940, p. 48) assert that the concave side of certain first instar *Opius* is the dorsal rather than the ventral aspect. I did not inquire into this point in the instance of *Opius* spp. from *Rhag. basiola* in rose hips.

Initially, the first instars are wholly enveloped in a thick layer of a gelatinous, grayish white substance composed of minute granules or spherules. Similar envelopes have been reported for *Opius humilis* Silv. and *Opius fletcheri* Silv. by Pemberton and Willard (1918) and *O. ilicis* Nixon by Cameron (1941). Cameron describes the substance as "a loose mass of large serosal cells with large nuclei," thereby indicating it originates in the embryo of the parasite.

As a consequence of enlargement of the parasite by feeding, and presumably also from contact with structures in the host, the envelopes of first instar *O. rosicola* and *O. baldufi* break here and there, and hang in tatters, and are, in a few days, entirely lost, leaving the body bare. Similar envelopes do not recur on subsequent instars.

Boese (1936) described what may have been similar envelopes around hymenopterous parasites in lepidopterous hosts. For example, he reported that the first instars of *Apanteles glomeratus* (Linn.) in the larva of *Pieris brassicae* (Linn.) become encysted by phagocytic haemocytes which undergo mitosis, forming a capsule of cells around the parasite. He observed further that the larger parasitic larvae are not subject to such attack.

The changes in form and size observable as the first instar of *Opius* develops from its newly hatched to its latent molting state results largely and directly from the ingestion of much food material from the host's body cavity. This dilates the alimentary canal which, in turn, presses outward against the body wall to enlarge the entire larva, excepting its head. The food taken by the first instar consists always of a pale yellow fluid, which is probably host lymph, and golden yellow globules of many

sizes suspended in the fluid. The globules are probably free fat originating in the fat body of the host.

Larval diapause. After feeding for an undetermined time, but perhaps a week, the first instar attains its maximum size and sacklike form. Then a curious phenomenon is observed. Whereas most immature insects which have reached the advanced phase proceed quite promptly to molt and continue their growth, the first instars of *Opius baldufi* and *O. rosicola* persist in their latent molting condition for periods varying probably from a few days to a few weeks. The duration depends on the age or developmental state which the host has reached when the female *Opius* introduces her egg. The parasite may persist in the latent molting state for several weeks when the egg is placed in a first instar of the host, or only one or two weeks or a few days when the host attacked is a second or third instar.

The persistence of the *Opius* in this advanced, molt-ready or latent phase of the first instar, although of variable duration, constitutes a true diapause. How the diapause is initiated remains unknown, but presumably by some physiological factor—possibly a juvenile hormone, produced in the parasite itself. This inhibiting agent occurs in all the first instars of *Opius* spp. in *Rhag. basiola* and invariably suspends their further development, usually for a matter of a few weeks.

The nature of this diapause differs from most delays known among insects in that its termination appears to be effected by some factor operative in the host. This belief was indicated by the results of dissections of several large samples of larval and puparial hosts. So long as the host remained in its larval stage in the hip, the parasite remained a first instar, although invariably attaining its latent phase. However, puparial hosts only three to five days old contained *Opius* that had molted and advanced beyond the first instar.

The coincidence of the molt of *Opius* and the prepupation of the host in the puparium suggests strongly that a hormone, produced by the host, activates the first ecdysis of the parasite as well as its own transformation to the pupal stage. More specifically, this molt of *Opius* probably takes place within a few hours after the full-grown larval host emerges from the rose hip and pupariates. In other words, the first instar and its diapause seem to terminate approximately at the inception of the prepupal phase of the host.

The suggested dependence of the parasite on the host for the stimulus to molt implies that the hormone-producing glands of *Opius* spp. have deteriorated functionally in a very long, well-adjusted relation with *Rhag. basiola*.

Advanced larvae. The exuviation of the dilated sacklike first instar

reveals a larva of very different structural characteristics (Fig. 18). The sclerotized head, the prominent falcate mandibles, the prosternal "mam-mae" and caudal processes of the first instar are lacking. The head remains somewhat quadrate, but is now like the rest of the white body in color and texture, and its anterior rounded face has a distinct vertical notch at the middle. There seem to be 12 postcephalic segments. These remain recognizably distinct until the pressure from much ingested food later obscures or obliterates their boundaries. The body is apparently bare, smooth and semitransparent excepting the area rendered opaque by the food and retained fecal matter. When removed from the puparial host, the larva lies on its side and, as then seen, is prominently and roundly humped above and concave beneath—a form reminiscent of the larva of the Colorado potato beetle. As seen from above, the total body has a mere sacklike shape, with the head narrower. Larvae of this form range from about 2.0 to 3.5 mm. in length.

It is likely that larvae of the above general type represent two instars. The final instar is distinguishable by its size—mostly 3.0 to 4.0 mm. long—its plump oval form, the relatively large speckles of white adipose substance under the cuticle, and its vestiture of numerous minute, uniformly short, close-set cuticular spinulae over the dorsum and perhaps other parts of the body. The spinulae arise from cuticular pits—the latter joined by minute grooves. Three pinkish red facial marks have been seen on some full-grown larvae, and presumably occur on all. These may represent structures of the pupa foreshadowed within the larval cuticle.

First, it should be emphasized that the entire development of the *Opium* larvae, subsequent to the first stadium, takes place within the puparium of the host. It is initiated with the molt of the first instar, and terminates with the eventual complete consumption of the host fat body. The exuviae of the first instar may usually, with but little search, be found near the young second instars. If newly shed, the discarded cuticle commonly remained entire, with a longitudinal break in the thoracic terga. Sometimes head and postcephalic parts were found separated. This larval form is readily obtained by prying one end off the puparium and pressing it with needles, causing the larva, which is then still much smaller than the host lumen, to slither out into a bit of water in the dissecting dish. The parasite then contains varying amounts of yellowish fluid and globules of fat that dilate the blind alimentary tract to various extents. This form is retained, but with increase in size, until the final instar is reached.

The growth of the parasite to the final instar within the puparium is unusually rapid, when compared with the long duration of the first stadium. Dissections of numerous puparia varying from barely hardened to several days of age showed that the parasites had reached their maxi-

mum size and the final instar in about two to three days after their first exuviation. In this short time, the body enlarges so much that it fills the puparium snugly and makes the removal of whole specimens difficult. The extreme dilatation of the body to its full size results from ingestion of the disintegrated fat body of the host. The body cavity of puparial *Rhag. basiola* normally is filled with such particles of fat body. These are readily sucked into the tract of the *Opius* larva, with apparently little immediate change in their form. The process appears to be essentially mechanical, and may be likened to the siphoning of a fluid from one barrel to another. The increase in size of the body through the two to three days may perhaps therefore be described as enlargement or dilatation, rather than growth. At any rate, the removal of the voluminous fat body is so complete that the host is now dead, with only the chitinous organs remaining depressed within the puparium.

This dilated state of the full-grown parasite is not tantamount to maturity. The ingested food gradually becomes reduced in volume, and as it presumably undergoes chemical modifications in digestion, it changes also from a yellow to a dusky brown contracted soupy mass, or meconium. Now the shrunken mature larva, filling the host lumen loosely, and enveloped in the host's tough unbroken larval cuticle, is easily extracted in a whole state from the puparium. In this matured state, the parasitic larva exists during the ensuing fall and winter.

When dissecting puparia to obtain parasites, I sometimes recorded the direction in which the mature *Opius* lay headed within. No one position proved to be taken, but most of those observed lay headed toward the cephalic end of the puparium. It was noted also that the walls of parasitized puparia are usually thin, brittle and dull yellow as compared with the thicker, harder stramineous walls of parasite-free puparia, or such as contain first instars.

A second diapause. It was stated above that the first instar of *Opius* persists in its latent molting state for periods of varying length, and that the termination of that diapause appears to depend on stimulation from hormones in the prepupal host. A second diapause begins with the maturity of the last instar of *Opius* in late summer to fall. It persists as such a full-grown final instar in the host puparium until spring of the next year, when it terminates in pupation after a duration of up to nine months. Inasmuch as the host has then been long since consumed, such hormonal stimulation as may be presumed to break the diapause in the next spring must originate within the parasite itself, incident to its larval-pupal transformation.

Precocious and delayed development. Four examples were discovered in which the opiine parasite completed the development from egg

to adult within the summer and fall of one calendar year. All originated in hips of *Rosa blanda* and *R. carolina* taken at Chetek, Wisconsin. The hosts pupariated in September and October, at Urbana, and the parasites proceeded to pupate without the usual winter diapause in the last instar. Two of the four were found in 1948, two in 1951. The two hosts of 1951 pupariated on September 24. When dissected on September 30, each contained a female pupa of *Opius*, whose eyes had turned brown, indicating that development to the adult stage had begun. The four puparia had been stored in shell vials in artificially warmed rooms without adequate moisture. If these conditions induced the precocious pupation, the diapause of the full-grown larval *Opius* would seem to be unstable in character.

On the other hand, I discovered a few instances of delayed emergence of adult *Opius* from the puparia of *Rhag. basiola*. The adult state was attained a year later than usual. Presumably most of the additional year was spent in the mature larval state. Particulars surrounding these instances are lacking.

Pupa. The full-grown larva of *Opius* spp. spins a scanty meshwork of silk on the inner wall of the host puparium. Transformation to the pupal form occurs in the warmer parts of the spring season.

In the newly formed pupa, the abdomen is bright white, while the head, thorax, basal parts of the legs, the wings and the antennae are pale yellowish white. First structures to show changes from yellowish white are the compound eyes, ocelli and mandibles, which first turn pale red, and later maroon. The rest of the body passes through shades of yellow to the final brown, the abdomen being last to attain its mature color. The antennae extend caudad straight along the inner edges of the folded legs and the wing pads, and, being longer than the body, curl around the end of the abdomen. The short, sturdy ovipositor bends vertically upward.

Life cycle. Like their host, *Rhag. basiola*, *Opius rosicola* and *O. baldufi* complete one cycle in a calendar year, their several life stages necessarily lagging chronologically behind the corresponding stages of the host.

Puparia which originated in Saskatoon, northeastern Minnesota and northwestern Wisconsin yielded adult *Opius rosicola* at Urbana between June 22 and October 4, in the over-all period 1945 to 1951. Puparia from Alaska, northeastern Minnesota, Chetek, Wisconsin, Orono, Maine, and eastern Illinois, yielded adult *Opius baldufi* at Urbana between May 21 and September 21, in the same years. Accordingly, the emergence of adult *O. rosicola* extended through 96 days; of *O. baldufi*, 123 days. Actually, the spread of emergence in any one year and locality was considerably shorter than those numbers indicate; the extremes recorded for the several localities in one year were 11 to 79 days. It is worthy of

note that the three adult males from Alaska issued between May 21 and 28. This antedated the earliest emergence from any other source by about two weeks, hence may signify an unusual hereditary tolerance of low temperatures. In a few cases, emergence of adults was delayed to the summer of the second year after parasitization.

In the course of observations in the field at Eaglesnest, I discovered 19 adult *Opius* on *Rosa acicularis* and *R. blanda* (incl. *Macounii*) between July 31 and September 5, 1945 and 1946. It is probable that they are abroad both before and after these dates.

The rare discovery of live embryos in host larvae dissected suggests that the embryonic stage is very short. Other evidence indicates that the embryonic development is completed in less than 24 hours.

Allowing some days for preoviposition and the retarding effects of northern latitude, the above data indicate that adult *Opius* are abroad parasitizing the larvae of *Rhag. basiola* at Eaglesnest chiefly from July into September. Further evidence on the time of oviposition is afforded by the dates of occurrence of unfed first instars of *Opius* less than 1.0 mm. long and still enclosed in their complete jelly-like envelopes. Larvae of this description were found at Eaglesnest between August 5, 1946, and September 11, 1949. Since the embryonic period may be less than one day in length, the dates of oviposition and of hatching are practically identical.

As stated above, the first instars of these *Opius* species may be present in any of the three instars of *Rhag. basiola*, but never in the puparia. Since the host larvae occur from July to October, the first instars of *Opius* are potentially present in these months. At Eaglesnest, I took the first instars during August and September, but, since investigations there had to be terminated before mid-September, the latest dates of their occurrence were not learned.

The instars beyond the first are confined to the host puparia, and complete their development within two to three days after pupariation, destroying the host before it reaches the early phase pupal stage. Pupariation of the host is known to occur from mid-August to late fall in the over-all area investigated. Accordingly, the *Opius* larvae become full-grown from August to October. These full-grown parasite larvae also form the wintering stage, hence may be present from August to late spring and mid-summer of the ensuing year.

I did not learn the duration of the pupal stage of individuals. The records relating to the emergence of the adults indicate that, excepting a few precocious individuals, pupation in the generation as a whole may occur from May to October, but ordinarily through late June to mid-August. Accordingly, the adult *Opius* appears from June forward, when the host has again attained the larval stage essential to parasitization.

Halticoptera rosae Burks, Pteromalidae, Hymenoptera

Types and sex ratio. This new species ranks with *Opius rosicola* and *O. baldufi* in importance as a parasite of *Rhag. basiola*. It was described by Burks (1955) from 58 females and 48 males. Six of the female paratypes and three of the male paratypes originated at Newport, Rhode Island in 1943 and 1944. The rest of the types were reared by me from hosts taken at various places in Wisconsin and northeastern Minnesota in 1945-1951. In those years, I reared 1,089 adults of *H. rosae* from places and rose hips named below. The sample consisted of 551 females and 538 males.

Hosts and distribution. My series of adults, and numerous larvae dissected from the hosts, originated entirely in stages of the rose hip fly, *Rhag. basiola*. According to Burks (1955), the U.S. National Museum has specimens reared at Newport, Rhode Island, from *Rhag. basiola*, also others from *Rhag. alternata*. Subsequent to the publication of his article, Doctor Burks informed me by letter that the record from *Rhag. alternata* is an error and should read "*Rhag. basiola*" instead. Stone (1951) regards these flies as distinct species. All the *Halticoptera rosae* reared to date therefore appear to have originated in *Rhag. basiola*.

The species of *Rosa* and the localities from which *Halticoptera rosae* is now known to me are as follows:

Rosa acicularis vars. Fairbanks and Big Delta, Alaska; Eaglesnest and Ely, Minnesota; also at several points along the north shore of Lake Superior, Minnesota.

Rosa blanda vars. Eaglesnest and Bally Creek, near Grand Marais, and Tower, Minnesota; also Chetek, Sarona and Gordon, Wisconsin, and Ottawa, Ontario.

Rosa arkansana. Chetek and Madison, Wisconsin.

Rosa carolina. Chetek, Wisconsin.

Rosa lunelli and *R. Macounii*. Saskatoon, Saskatchewan.

Rosa woodsii. Beulah, Manitoba, and Provo, Utah.

Rosa virginiana. Orono, Maine; Newport, Rhode Island (Burks, 1955).

Rosa rugosa. Newport, Rhode Island (Burks, 1955).

The specimens from Newport were secured by Mayer, Kisliuk, and Mallia.

These data show that *Halticoptera* occurs at least from Alaska on the north to Madison, Wisconsin, and from Provo, Utah, eastward to Ottawa, Ontario, and Orono, Maine. Although numbers of *Rhag. basiola* were reared from hips of several species of roses, including *R. virginiana*, *pallustris*, *canina*, *eglantaria*, *gallica*, *carolina* and *setigera*, in Ohio, Indiana, and eastern Illinois, this chalcid was not obtained. According to these evidences, *H. rosae* ranges southward to approximately the Wisconsin-

Illinois state line, and appears to be more limited in distribution than its native host, *Rhag. basiola*.

The adult. The characters given herewith are selected from the detailed description prepared by Burks (1955), and will serve to distinguish *Halticoptera rosae* from other chalcids obtained from rose hips.

Female (Fig. 19). Length 3.5 to 4.0 mm. Head black with bright green or faintly brassy metallic reflections; antennae mostly very dark brown, scape dark, metallic green; thorax above bright metallic blue-green; pleura and sterna black with faint brassy reflections; propodeum bright metallic green; abdominal petiole and gaster black with faint metallic green reflections.

Male. Length 3.0 to 3.5 mm. Head and thorax bright metallic green; antennal scape yellow at base, shading to tan at apex, pedicel dark at base, distally golden tan, funicle uniformly golden tan, club slightly darkened; enlarged terminal segments of maxillary palpus slightly longer than wide, apex of terminal segment nipple-like and hirsute.

Egg (Fig. 22). Length about 0.2 mm., apetiolate, pale whitish, chorion smooth; narrowly rounded at the caudal end, with gradual widening to the broadly rounded cephalic end.

Larva (Figs. 23-27). The newly hatched first instars (Fig. 23) before feeding are from 0.2 to 0.25 mm. long. In their mature state (Fig. 25), they attain a length of 0.6 to 0.9 mm., and a corresponding increase in diameter. The body of this instar is approximately fusiform, broadest in the thoracic region, tapering abruptly toward the head but gradually toward the cauda. The head is somewhat longer than wide, suboval in dorsal view, pale brown and lightly sclerotized, with the oral aperture subapical and ventral. The thorax and abdomen appear to comprise 13 segments, but sometimes there seemed to be 12, perhaps due to the retraction of the small terminal member. The first two thoracic segments are bare, but the metathorax and each of the abdominal segments bears a transverse series of several spines on the dorsocaudal margin. The small terminal segment is distinct in that it bears spines of diverse lengths on its ventral side.

Of the internal systems, only the alimentary tract is macroscopically visible, due to the opacity of its food contents. It appears to be a simple undifferentiated sack, narrow in the head and bulging little to much in the abdomen, depending on the amount of the contained food or waste. It remains closed behind, and extends caudodorsad to terminate blind in what appears to be the tenth postcephalic segment.

I did not determine the number or characteristics of the instars that develop after the first molt. But the advanced larvae differ sharply from the first instar in form of body. Newly molted second instars (Fig. 26)

are about 1.2 mm. long, 0.6 mm. wide, with smooth, shiny cuticles and few or no small speckles of whitish adipose visible through the cuticle. This larva soon becomes sacklike, dilating increasingly as more host substance is ingested, and, as a consequence, the segmental lines of thorax and abdomen become obliterated.

What I take to be last instars of *Halticoptera rosae* (Fig. 27) are 1.8 to 3.2 mm. long, robust, with 13 postcephalic segments; the head is short and retracted into the thorax, and the abdomen terminates bluntly and bends slightly ventrad at the apex. These larvae are wholly white, with a pearly luster, bare, smooth, with prominent transverse rounded dorsomedian ridges and bunlike pleural swellings on the thoracic and abdominal segments. Many small white speckles of adipose appear under the cuticle.

The size and number of the speckles, the presence of ridges and swellings, and the absence of spinulae on the pearly cuticle distinguish the full-grown larvae of *Halticoptera* from those of *Opius* as these are found in the puparia of *Rhag. basiola*.

Emergence and movements. The young adults escape by gnawing a subcircular hole through the side near the apex of the puparium as do also the adults of *Opius* spp. In the field, they were observed at rest on rose plants, and also moving deliberately over leaves and buds. Their locomotion is a combination of jumping and flying for short distances.

Mating and oviposition. Apparent attempts at mating by one-day-old individuals that issued from puparia in captivity were observed in several instances. Whether coitus occurred, it was impossible to ascertain. However, the observed impulse suggests that copulation may occur very early in adulthood and that the activity is of very short duration.

In June, 1945, I discovered a chalcid, later identified as *H. rosae*, apparently engaged in ovipositing into a hip of *Rosa acicularis* in the field at Eaglesnest, Minnesota. Dissection showed the chalcid was working at a point where an egg of *Rhag. basiola* had been inserted, and also that the egg contained a minute living larva. By exposing fly eggs, laid in captivity, to reared females of *H. rosae* 11 days old, I established that the minute larva was indeed that of this chalcid. It demonstrated too that the green chalcids which emerged from puparia of *Rhag. basiola* institute the parasitic aspect of their life by inserting their eggs into those of the rose hip fly implanted into the hypanthia of the rose hips; also that the resulting larvae hatch within the embryonic host. These preliminary findings were confirmed hundreds of times in the years 1945 to 1951 by the discovery of such parasitic larvae in host embryos and larvae dissected from hips.

The female of *H. rosae* discovered on a hip in June, 1945, rapidly

tapped the locus of the fly egg with the apices of the antennae. Then several minutes were spent in stepping alternately forward and backward over the egg site, meanwhile palping the place with the antennae and applying the abdomen to it as if attempting to insert the ovipositor. When the host was examined four days later, the parasite had already hatched within it.

In subsequent observations, it was disclosed that the eggs are placed free within the body of the host embryo, i.e., not attached to any interior structure. I have found the eggs of *H. rosae* in the early, the intermediate and the advanced phases of the host embryo. But since the "egg" stage of *Rhag. basiola* appears to last as much as 40 days, and the embryo is in its advanced phase probably eight-tenths of this period, the female *H. rosae* chances to place the large majority of her eggs in the advanced form of the host. The egg is inserted shallowly into the cauda of the host embryo, as is shown by the consistent occurrence of the young first instar in the posterior quarter or fifth of the first instar of *Rhag. basiola*.

The above lone instance indicates the so-called "egg stage" is less than four days, and probably one or two days, if not mere hours, in duration. That it is brief is shown also by the discovery of very few embryos as compared with many newly hatched larvae in the host embryos scrutinized.

"Brown bodies" (Figs. 20, 21). In dissecting the eggs, three instars and the pupae of *Rhag. basiola* I found, not infrequently, small inert bodies which, after considerable puzzlement I identified as dead eggs of *H. rosae* (Figs. 20, 21). The best-preserved specimens retained the form of normal eggs and contained recognizable amounts of gray granular yolk, yet no clear evidence of embryos. Older eggs had collapsed, with the terminal thirds medium brown and the intermediate third pale brown, while still older specimens had collapsed completely, turned dark brown and sometimes became more or less curled or twisted, corkscrew-like.

The increase in their numbers as the summer advanced, and failure to find embryos in these bodies, seem to mean the eggs were not fertilized and that the sperm supply for the late-season or old females may have been exhausted. This condition might develop in species, like *H. rosae*, that exhibit a distinct protandry, with the consequent absence of males when the late fraction of females emerges from the host puparia.

These "brown bodies" are comparable, as to their origin, to those described above for *Opicus*. They were more numerous in *Halticoptera*.

Larval life. The parasite hatches within the embryo, not in the first instar, of the host. This is what may be expected since embryonation of

the parasite is completed in a few hours or days, whereas that of the host seems to require about 40 days.

Among numerous first instars of *H. rosae* obtained by dissection from the eggs of *Rhag. basiola*, only one was taken in the process of hatching. The infrequency of this occurrence in itself indicates that the "egg" stage is short and the activity of hatching of brief duration. In the one case discovered, the posterior three-fourths of the parasite still lay enveloped in the translucent chorion. By means of bodily pulsations and feeble writhing, the larva extricated itself from the chorion.

One parasite per host embryo is the predominating condition, but two are not infrequently present. In some cases of duality, one parasite was found dead, but I have seen no evidence of cannibalism; moreover, the probability that the parasite feeds little, if any, in the host embryo, indicates that death is not due to competition for food supply. Further, not uncommonly a single host embryo contained a living parasite and also one or two brown bodies, or two brown bodies alone. In the extreme instance of multiple parasitism noted (discovered on August 7, 1945, at Eaglesnest) an advanced host embryo simultaneously contained two brown bodies and two living, newly hatched first instars. Eventually, all supernumerary parasites die. I have no evidence to show that a host can support more than one parasite to maturity.

First instar. When the parasitized host embryo hatches to become a free-moving, boring larva in the hypanthium of the rose hip, it contains in its body cavity the small, early phase instar of *H. rosae*. Soon the supply of pale white yolk which it carries over from its embryonic state seems to be depleted, for the young instar of a few days of age contains substance it has ingested from the first instar host. Its alimentary tract contains a pale yellowish fluid, probably blood plasma, in which are suspended globules of rich yellow material that vary much in size and probably represent droplets of fat from the host's fat body.

The rate of ingestion of host substance is very slow or small. The parasite increases in size, but slowly, multiplying its bulk as a first instar by four to five times while the host grows from a young first instar about 1.0 mm. long to a mature larva about 8.0 or 9.0 mm. long. The amount of material ingested is such that the growth of the host is not visibly retarded in any of the instars. The *Rhagoletis* soon attain a plump appearance despite the presence of the first instar *H. rosae*, and I have no conclusive evidence that mortality from normal parasitism occurs in host larvae of any instar. Many young first instars of the hip fly die when they inhabit the very hard hypanthium of some rose hips, but usually these are parasite-free.

As the weeks of August, September and October pass, and the host

larva develops from the first to the third instar and transforms to the early pupal phase in the puparium, the larva of *H. rosae* persists as a first instar. However, during this span of weeks, this first instar slowly, gradually increases in size, and acquires a sharply different shape, yet basically identical form of body (Fig. 25).

It has now added much bulk in the postcephalic region, while the head retains essentially its original form. The dorsal and caudal spines, as well as the general fusiform outline, attest to the fact that this is still the first instar. Its enlargement appears to result basically from a gradual inflation of the digestive tract to its full capacity; the dilated tract in turn swells the body wall and seems to occupy all the space of the body cavity.

Why is the development of the first instar of *H. rosae* so slow as to require a period of time that corresponds in length to almost the total larval life of the host? By way of answer, I propose a theory based on the nutrition and mouth parts of the parasite. The three host instars inhabited by the first parasite larva contain a normal fat body of web-like form. It is possible that, owing to the structure of its mouth parts, the parasite cannot acquire the particles of the fat body as bound in the webbed state, and thus must utilize blood plasma and such host fat as floats free in the blood. This implies that the substance of the fat body is more effective than plasma and free fat as a promoter of growth, but is not available to the parasite owing to its type of mouth parts.

Diapause. The first instar of *H. rosae* involves two life phases. The first is characterized by the function of feeding-growing, and occurs entirely in the host larva. This phase terminates with the full-fed state of the first instar, an event of late summer or fall. The second, or diapausing phase begins with the termination of the feeding-growing phase, and persists after the host larva pupariates in late summer to fall, and while the host winters in its early pupal phase. At approximately the time when the host resumes its pupation in May or June, the diapausing parasite finally molts to the second instar. The supposed precise concurrence of the molt and the resumption of pupation of the host suggests that the pupational hormone may trigger the molt of *Halticoptera rosae*. These phases of the first instar are emphasized to stress that the first phase is not a diapause, even though, due to the very slow and prolonged growth, it may superficially appear to be such.

Phagocytes and the first instar. Whereas the young first instars of *Opius* are invariably enveloped in a gelatine-like substance, only a few *Halticoptera* were found so enwrapped, and these were not young instars. In seven years, I discovered, by dissection of hosts, only four such cases. Whereas the gelatinous substance enveloping *Opius* was never

fatal, that enveloping *Halticoptera* destroyed the parasite. All the four were found in September, and had developed to the advanced or diapausing state and occurred within living puparial hosts one to seven days of age, i.e., either prepupae or early phase pupae. In three of the four cases, the parasites were dead, brown, somewhat shrunken, and completely enveloped with the gelatine-like material. The body of the fourth was smooth and turgid, the head and the anterior part of the thorax remained free and lifelike, and pulsations indicative of life persisted in the thoracic part of the body cavity. But a large part of the enveloped abdomen had turned black and was presumed dead.

Since the phagocytes, presumed to be active in these instances, occurred in the host puparia, it is possible they may have been identified in some way with the process of histolysis which transpires incident to pupation of the host. But the fact that only a few of the parasites found in the puparia were affected in this manner indicates that the above victims of phagocytosis, or the phagocytes themselves, were unusual in some way.

"Milky" first instars. Only in the fall of 1951, I discovered a number of advanced first instars of *Halticoptera* at Eaglesnest, Minnesota, and Chetek, Wisconsin, which appeared normal except they were subopaque and diluted milky white. The affected parasites measured 0.6 to 0.9 mm. long, and varied from slenderish to plump in form, and inhabited puparia 2 to 25 days of age that contained prepupae and early phase pupal hosts. In the same year, many first instars from the same geographic sources were normal in color.

Advanced larvae. As already stated, the first instar of *Halticoptera* is terminated with the molt that takes place in the spring season at about the time the host resumes its postwinter pupation. By now the adipose web of the pupal *Rhagoletis* is normally disintegrated, and appears creamy in texture, and the second and later instars of the parasite obviously possess a suctorial type of feeding organ which permits quick ingestion of relatively larger amounts of food than the first instar is able to take. This homogenized adipose may also be highly nutritious. At any rate, the parasite grows apace and attains its full size in probably only a few days, i.e., in much less time than was required for the growth phase of the first instar alone. In the course of this rapid mechanical transfer of host substance into the parasite, the host is depleted and killed. The rapid rate at which the bulk of adipose is conveyed into the parasite suggests that it undergoes little chemical change at once, and that therefore the enlargement of the parasite does not constitute true growth. This physical dilatation is followed later by physiological maturity, for the parasite, first greatly distended with food, shrinks per-

ceptibly in time as the ingested adipose changes from yellow to greenish, dull brown or purplish. These changes indicate that the nutrients are gradually absorbed from it, eventually leaving the indigestibles in the form of a dark contracted semisolid mass in the peritrophic membrane.

Contraction waves. Upon opening a puparium of *Rhagoletis* in May, I discovered a second instar of *H. rosae* 1.55 mm. long, the actions of whose digestive tract were readily observable. In nine minutes and forty seconds, the walls of the tract completed 31 contraction waves. These ran the full length of the tract and thoroughly churned the adipose newly ingested from the host. The individual waves required from 10 to 40, but mostly 14 to 25, seconds to run their full course. Twenty-five of them proceeded from head to cauda; only six from cauda to head. Predominance of the cephalocaudal waves seems to expedite the removal of food from the oral area into the midgut.

Similar waves were also seen in an early first instar in the embryo of the host. The food in the digestive canal was probably derived from the parasite egg, and flowed alternately backward and forward as the larva shortened and lengthened itself by means of contractile movements in its postcephalic segments.

Pupa. The meconium is discharged incident to the prepupal molt that discloses the newly formed white pupa. It appears that the full-grown larva does not spin a cocoon of silk, so that the pupa lies bare in the empty puparial shell of the host.

Life cycle. *H. rosae*, like *Opium baldufi*, *O. rosicola*, and their host *Rhagoletis basiola*, completes one cycle or generation in a year.

At Urbana 1,034 adults of *H. rosae*, reared from host puparia, emerged between June 2 and July 31 in the over-all period of 1946 to 1951. All originated in areas north of Illinois.

The retarding influence of northern climate on dates of emergence is reflected in the case of two lots of puparia which originated and wintered at Eaglesnest, Minnesota. These yielded adult *H. rosae* from July 7 to August 26, 1946, or four to five weeks later than their counterparts wintered at Urbana. Adults were seen in the field at Eaglesnest between August 6 and 31, 1945, and eggs were found in the host embryos as early as June 30, 1946, and as late as September 6, 1945. At Eaglesnest, Minnesota, *Halticoptera rosae* places her eggs into those of *Rhag. basiola* between late June and late August. Embryonic development appears to require less than four days, and the larva persists, apparently making little or no growth, in the host embryo for varying lengths of time, since this host stage may have a life as long as 40 days. The first instar of *H. rosae* is a slow-growing parasite, developing from the newly hatched state to its much dilated mature phase while the host larva grows through

all its three instars; this, I have calculated, requires about 30 to 35 days. The larva of *Rhag. basiola* becomes full grown, emerges from the hip, and pupariates beginning about mid-August. After three to five days in the prepupal stage, the host enters its early pupal phase, a true pupa, and invariably enters into diapause. In the absence of parasites, the process of pupation is resumed and completed in the subsequent months of May to June.

While the host winters as an early phase pupa, the parasite persists as a mature first instar. The next advance in the development of the parasite occurs in May to June. It then molts to the second instar; this molt appears to be concurrent with the resumption of pupation of the host, and, moreover, may be dependent on it in the sense that the host's pupational hormone may also trigger the molt of the parasite. The development of *H. rosae* through all the instars following the first is completed rapidly, certainly in less than a week. These instars feed upon the adipose of the host pupa, which substance is now in disintegrated, easily available form; this may be a major reason why these instars grow relatively rapidly. Thus, the host is killed as a pupa in late spring and early summer, and the matured parasitic larva pupates in the puparium.

Accordingly, the total larval stage of the *H. rosae* utilizes three successive major metamorphic stages of the host—embryo, larva and pupa—in its development.

Chronology of Rhag. basiola and its parasites. This statement is based on the dates of emergence of the adult *Rhag. basiola* and the adults of *Opius* and *Halticoptera* from puparia in the years 1946, 1947, and 1948. They were reared in approximately natural temperatures at Urbana, Illinois. All but a few of the host puparia originated in northeastern Minnesota. From the dates of earliest and latest emergence in the three years, it follows that the adults of *Rhag. basiola* issued between May 28 and July 10; those of *H. rosae*, between June 10 and August 10; and of *Opius rosicola* and/or *O. baldufi* between June 30 and August 6 and forward. While a considerable amount of intergeneric overlapping is indicated, this is not so significant as it appears to be, for the late dates commonly involve only very small fractions of the totals reared, or occasional stragglers. The large majority of each group emerged within narrower time limits than those indicated, and when viewed in terms of these majorities, the periods of emergence of the host, *H. rosae* and *Opius* spp. prove to be fairly distinct.

The order of seasonal appearance of the adults is then as follows: the host, *Rhag. basiola*, *H. rosae* and *Opius* spp. *H. rosae* can begin its parasitization earlier than *Opius*, since it utilizes the host embryo, that

may last forty days individually, while *Opius* oviposits in one of the subsequent larval instars of the host. The fact that *Opius* spp. diapause and winter as full-grown larvae, whereas *H. rosae* does so as an advanced first instar, may at first lead one to anticipate that *Opius* has a head start, developmentally speaking, and therefore might be expected to become adult decidedly before *H. rosae*. That this is, however, not the actual sequence of events provokes the theory that the chalcid early resumes its larval development in the spring due to stimulation from the pupational hormones of its living host, whereas *Opius*, inhabiting the dead empty host puparium, is dependent on its own hormonal stimulation alone, and thus comes out second to *H. rosae* in its advance to adulthood.

Eupelmidae spp., Hymenoptera

In the years 1946 to 1951, I obtained 13 small larvae that performed as solitary endoparasites in the three instars and puparia of *Rhag. basiola*. The similarity of the first instars to Clausen's illustration (figure B, p. 198:1940) suggest they may be a kind of eupelmid chalcid. In the same years, I had a series of adults of a *Eupelmus* sp. from quantities of hips picked at Eaglesnest, Minnesota, and in Wisconsin, and Illinois. Whether these larvae and adults represent one and the same species was not established.

Larvae from Rhag. basiola. The first instar (Fig. 47) of this supposed eupelmid differs noticeably from the first instars of *Halticoptera rosae* and *Opius* spp. Length 0.5 to 0.8 mm. Head pale brown, wider than long, broadly rounded in front, sides subparallel, about as broad behind as base of thorax; a transverse row of at least two pale spines on sternum of each of first six, or more, postcephalic segments; similar spines also on terga of some segments; abdomen narrowing behind and terminating in a pair of identical, flexible, depressed pointed processes which curve ventrad and diverge strongly at their apices.

Figure 48 illustrates what I take to be the second instar. Lengths observed were 1.2 to 2.0 mm. The head is concolorous with rest of body, short, bilobed in front; postcephalic region much dilated, broader and longer than that of first instar; abdomen sacklike, soft, with a caudal pair of short, pointed processes, one at each outer posterior angle. One such larva appeared to have 12 postcephalic segments, these being rather obscurely demarcated due to inflation of body with food.

These parasitic larvae were found in *Rhag. basiola* that originated in northeastern Minnesota. Six living first instars occurred in host larvae of the first and second instars and in mature emerged larvae and in puparia one day old. The second instars inhabited puparia five days old. All the larvae were discovered, by dissection of hosts, between August

21 and October 3. Because the first instars appeared in first instars of the host, the female presumably oviposits either in them or in the eggs. Moreover, the persistence of first instars in one-day puparia, and the presence of seconds in five-day-old puparia suggests that the parasite may delay its molt to the second instar until the host enters its prepupal period. In other words, this is possibly another instance wherein the parasitic first molt depends on stimulation of a sort from the host, as was observed in *Opius* and *Halticoptera* in *Rhag. basiola* above.

Eupelmus from hip jars. The 18 adult individuals obtained alive from hips originating at Eaglesnest, Minnesota, Chetek, Wisconsin, and two localities in Illinois, appeared in hip jars between August 16 and September 30 of four years, excepting one (Taylorville, Illinois) which emerged on May 27. The two Illinois specimens came from localities and hips that rarely or never yielded the rose hip fly; this fact casts doubt on the supposition that *Eupelmus* sp. is the adult of the Eupelmidae? sp. larvae found in this fly.

THE ROSE HIP MOTHS, *Cydia* spp., OLETHREUTIDAE, LEPIDOPTERA

In the earlier literature, these small hip-inhabiting caterpillars are referred to generally under the names *Grapholitha*, Tortricidae, but in later publications as *Cydia*, Olethreutidae. Accordingly, they are near relatives of the codling moth, *Cydia pomonella* (L.) and the oriental fruit moth, *C. molesta* (Busck), and resemble these species in mode of life, and especially in that they inhabit and ingest the pulpy parts of rosaceous fruits. Among the phytophags that inhabit rose hips, they are bionomically comparable to the Trypetidae, *Rhag. basiola*, *Rhag. alternata* and *Carpomyia Schineri*, in that they limit their activities as larvae to the flesh of the hip, thereupon emerging to pupate externally. Two species of *Cydia* are known to sustain such relations to rose hips, namely the American form, *C. packardi* (Zell.), now officially called the cherry fruitworm, and the European form, *C. roseticolana* (Zell.).

Cydia roseticolana (Zell.)

The early synonymy is given in Zeller (1871), Eppelsheim (1871), and Staudinger and Rebel (1901). Zeller (1849) described *C. roseticolana* from a female obtained from Tuscany. The literature listed by Zeller (1871) records this species from Breslau, Baden, at Halle an der Saale, Nassau, at Glogau, Oesel, Schlesia, Meseritz and Stettin, Germany. Eppelsheim (1871) had it from Grünstadt, Germany, and Barrett (1872-73) recorded it as *Endopisa roseticolana* from Britain. A more thorough investigation will probably show it occurs widely in northern Europe.

Little appears to have been published pertaining to the life history. The principal observations were made within the quarter-century after Zeller (1849) named it in the genus *Grapholitha*. Zeller (1871) and Eppelsheim (1871) made known such basic facts as we have today. Kaltenbach (1874) quoted the observations of Eppelsheim in his book on insect enemies of plants. *C. roseticolana* is the only insect from rose hips treated by Lüstner (1931) in an extension circular dealing with the most important enemies of rose in Germany.

At Grünstadt, Eppelsheim found the larvae as early as the middle of August in the fruits of *Rosa canina*, a scattered but omnipresent plant. The larvae eat their way into the hip just below the crown at the base of the calyx. The point of entrance is easily recognized as a small black spot. While they are small, the mines are indicated as dull pale brown areas in contrast to the undamaged parts of the hips. As they grow, they gradually destroy the hip flesh; hence the surface wrinkles, sags and becomes dark-spotted. In August to September, 1870, Eppelsheim secured 400 to 500 inhabited hips, from which the mature larvae emerged later that year. According to earlier reports by Koch, v. Heinemann and Rössler, the mature larvae were supposed to enter the ground for pupation; but, seeing one boring into the end of a dry rose stem in the field, Eppelsheim gathered dry stems of *Eryngium campestre* L. to further test his field observation in the laboratory, and soon was gratified to see that numerous larvae entered these stems. They prepared burrows 1.5 times the length of their bodies and just wide enough to permit them to turn end for end. The entrance was walled off from the outside with a silken web.

At Meseritz and Stettin, Zeller (1871) also found the larvae in the hips of *R. canina*, but not in "rose galls," as Scholz claimed (Zeller, 1849). About the middle of September, he reared many larvae from red rose fruits. Black patches on the fruits indicated inhabitation by larvae. These remain in the hip until full-grown. Much excrement is voided into the burrows, which is at first light red, later, when dry, red-brown. He also observed that they do not eat the achenes of the hip; i.e., they confine their activity to the hypanthium.

Upon emerging from hips in a rearing jar, some larvae spun themselves in with silk, but most of them dried up, which indicated that the natural cocooning site was lacking.

The mature larvae are 8 to 9 mm. long and pinkish. Eppelsheim reported seeing dark spots on the dorsum of the eighth body segment. I presume these were the incipient testes of the adult male moth.

The larvae observed by Eppelsheim wintered as such, and pupated in late winter and early spring, in an artificially warmed room. The chrysalises, excepting the last abdominal segment, emerged from the

cocoons shortly before the moths issued, from April forward. Zeller (1871) reported the same movements of the pupae, and also the emergence of one adult on May 13. He adds emergence records for May 22, and also June 6, and presumed the natural flight period begins in the last third of May, and had observed it to extend throughout June.

The above data indicate that *Cydia roseticolana* has one generation in a year where observed, with the mature larvae as the wintering stage. I have seen no records of parasites attacking this species.

Cydia packardi (Zell.), The Cherry Fruitworm

Synonymy. Owing to its damage to the fruits of several cultivated plants, *C. packardi*, named and described by Zeller (1876), has been comparatively well investigated and a considerable body of facts made known concerning its mode of life and host relations. Heinrich (1926) summarizes the principal synonymy of the species. Previous to 1950, the bibliographies largely employed the name *Grapholitha packardi* Zell., but *Cydia packardi* (Zell.) in the present decade. Sanderson (1900, 1903) called it "the apple bud-borer." However, the larva appears to prefer fruits to buds or twigs, and currently is rated as a pest in cultivated cherries. While wild cherry is clearly one of its principal native hosts, the hips of wild roses rank prominently as native food plants.

Distribution. Between 1945 and 1951, some thousands of individuals of *C. packardi* were obtained by dissection of immature larvae from rose hips, and by rearing mature caterpillars in hip jars and some adults from cocoons. Most lots of the source hips were secured personally, others through collaborators. By these means, *C. packardi* proved to occur in rose hips in the following areas: northeastern Minnesota, from the north to the south limits of Wisconsin, numerous localities of northern and east central Illinois, several widely placed points in Indiana and Ohio, in Guilford County, North Carolina, Geneva, New York, Nebraska, Missouri, Oklahoma, Kansas, Idaho, Washington, and Saskatoon, Saskatchewan.

The literature affords the following distribution records, few of which have reference to the species in rose hips: Texas, Mississippi, Missouri, Arkansas, Illinois, Michigan, Maryland, West Virginia, Virginia, New Jersey, Delaware, Massachusetts and New Hampshire (Heinrich, 1926); New York (Forbes, 1923); British Columbia, Canada (Downes, 1929, 1929a); Washington (Breakey and Webster, 1939, Newcomer, 1950); Iowa (Richardson, 1943); Colorado (Hoerner and List, 1952); Wisconsin (Dever, 1953); and Michigan (Vergeer, 1954).

Cydia packardi has a wide distribution in North America, the extreme points of its recorded occurrence being British Columbia, Saskatchewan,

Washington, Texas, Virginia and New Hampshire. Most of the records refer it to the region north of the latitude of the Ohio river.

Rose hosts. In northeastern Minnesota, the larvae of *C. packardi* were found to inhabit the hips of *Rosa acicularis* vars. and *R. blanda*, including *Macounii*; in Wisconsin, the rose hosts were *R. blanda* vars., *R. arkansana*, and *R. carolina* vars.; in Illinois, usually *R. carolina*, and sometimes *arkansana*, *palustris*, *virginiana*, *eglanteria*, *canina*, *setigera*, but not *hugonis*; Indiana, *R. carolina* and *palustris*; Ohio, *R. palustris*, *rubifolia* and *R. spp.*; Nebraska, *R. Macounii*; Missouri, *R. carolina*; Kansas, *R. suffulta*; Idaho and Washington, *R. spaldingii*; Saskatchewan, *Macounii* and *lunelli*. *C. packardi* has the same general range and rose hosts as *Rhag. basiola*.

Adult. The moth is dark grayish to brownish, with a wing expanse of about 10 mm. In describing "*Grapholitha*" *packardi* Zell., Heinrich (1926) states that "the adult is smaller than that of *G. molesta* and has a faint but distinguishable dark median fascia on the forewing. Its most striking character is a strong patch of blackish sex scaling upon the upper surface of the hind wing and a similar patch on the under surface of the forewing of the male. This character, so far as I know, is shared by no other North American species of *Grapholitha* or *Laspeyresia*." Forbes (1924) reported the adult from New York, under the name "*Laspeyresia pyricolana* Murtfeldt."

Egg and oviposition. The egg is 0.5 mm. in diameter, circular in outline, depressed, slightly convex, opalescent to yellow, the contents turning grayish white as they develop (Dever). I have seen a few empty pale grayish white chorions on rose hips. Their scarcity suggests that they may be ingested by the newly hatched larvae, or fall from the hip after hatching takes place. The moth obviously prefers natural depressions for oviposition. On rose hips, the eggs were usually placed in the rounded, necklike constriction at the apex or floral end of the hip.

In the case of cherries cultivated in British Columbia, the eggs are laid on the fruit, usually in the suture near the apex, but some at the basal or stem end (Downes, 1929). In Colorado, Hoerner and List (1952) found them deposited often in the suture or any rough spot on cherries, and sometimes around the stem, or on the stem close to the fruit. In Wisconsin, Dever (1953) usually discovered them "next to the suture at the base of the petiole or at the calyx and next to the pistil scar" of cherries. Observing this species in Michigan, Vergeer (1954) reported the eggs "often cemented in the groove between the sepal and the central disk of small blue berries." In contrast with the above observations that the eggs are laid on fruits, Garman (1918) reported they are placed on the upper and under side of the leaves of apple, in which case the resulting larvae bore into twigs.

Larva. The descriptions available in the literature presumably pertain to the mature larva. Murtfeldt (1891) described it in general terms, and Dever (1953) provides an illustrated technical account, including the setal pattern. In his article of 1954, Dever included setal maps and also the following verbal description: "Mature larva—general color whitish-pink, ventral surface not so pink as dorsal; head, from mottled yellowish-brown to dark brown, shiny; mouth parts, pale gray, almost white; antennae, white at base, slightly darker towards tip; thoracic shield, shiny, pale yellow to light brown, divided in the middle by a longitudinal paler line; thoracic legs, white; prolegs white, crochets uniordinal, uniserial, and in a complete circle; crochets on anal prolegs uniordinal, uniserial, and in a transverse band; setae on grayish-white pinaculae; anal shield, mottled grayish-black; anal comb, dark brown with four to six prongs of irregular length."

By dissecting buds and hips of *Rosa*, I obtained evidently newly hatched larvae hardly more than 1.0 mm. long, and pale in color. According to Vergeer (1954) larvae of the first stage are 2.0 mm. long, white, with a dark brown head; the head, thoracic shield and the anal plate become smoky brown as the larva grows, and at maturity it changes to bright reddish pink above while remaining decidedly lighter beneath. The full-grown larva bears an anal plate of three separate parts, and attains sizes varying from 5.0 to 9.0 mm. in length. From rose hips, I reared some female larvae 10.0 mm. long, and also individuals only 5.0 mm. long. The smaller sizes seem to result from undernourishment in unusually small hips, in deteriorating hips in the field or jars, and in hips shared by other larvae of their kind, or *Rhag. basiola*. I have no direct evidence that endoparasitism alone produces larvae of the smaller sizes. The pinkish coloration indicates impending larval maturity.

Among the larger larvae, the males may readily be distinguished by the paired clusters of reddish to purplish, wine-colored gonads situated in the dorsal area of the fifth abdominal, or eighth postcephalic, segment. Each cluster comprises four filbert-shaped bodies appearing attached to to each other by their edges. In one instance, among many gonads observed, one cluster of the pair consisted of five bodies, indicating that the testicular tubes of the adult may be subject to slight numerical variation.

The number of instars comprising the larva appears not to have been determined. Molts may be anticipated soon when the diameter of the thorax strongly exceeds the width of the head; on the other hand, a recent molt is indicated when the head and thorax are about equal in width, and the body color remains more or less pale.

Food and niches of the larva. Whatever their food plants, all the instars of *C. packardi* exist as borers, seeming to enter the plant directly

from the egg, and live invisibly within buds, shoots or fruits of the host, and appear not to feed first externally on leaves. Heinrich (1926) listed apple, rose and *Crataegus* as the food plants, and rated *packardi* as "a species of some importance as an enemy of apple. . . . It usually attacks the growing tips, seldom the fruits. It has also been reared from rose tips and there are a couple of doubtful records from peach."

However, it appears now to be more frequent and important economically in the following fruits: Cherry, particularly cultivated sour varieties, in British Columbia (Downes, 1929, 1929a); Washington (Breakey and Webster, 1939; Baker, 1930; Newcomer, 1950); Colorado (Hoerner and List, 1952); Wisconsin (Dever, 1953, 1954). Blueberry (*Vaccinium*) in New Jersey (Lipman, 1936; Tomlinson, 1951); Michigan (Vergeer, 1954). Apple, in Missouri (Murtfeldt, 1891); Delaware (Sanderson, 1900, 1903); Maryland (Garman, 1918); Iowa (Richardson, 1943).

I have found it to be a major species in the hips of roses in Minnesota, Wisconsin, Illinois, Indiana, and Ohio. The larva is unique among the major phytophags in rose hips in that it also utilizes rosaceous fruits other than roses, and also blueberry.

Larva in apple (Apple bud-borer). According to Murtfeldt (1891), whose record appears to have been the first for apple, the larva "bores the shoots of the second growth of apple in August and September, occasionally on recently planted trees, inflicting serious damage. The larva spins scarcely any web, but bores downward through the terminal bud, entering the stem from half an inch to an inch, sometimes blackening all the growing points of a young tree."

The mode of attack described by Sanderson (1900) is similar. On hatching, the larvae mine through the outer terminal leaves and bore down into the twig often for a distance of one or two inches. Then the twig dies, and new shoots grow from the first lateral bud below it. This new shoot is attacked, and so on, one new growth after another, until the twig has been badly stunted and given a zigzag, knotty form. Tender "water sprouts" on trunks of old trees are generally infested. Garman (1918) adds that the larva infests "apple fruit and twigs; peach, twigs," but the growing shoots of apple are its favorite food. On the basis of observations made at Bevington, Iowa, Richardson notes that the larvae seem to bore only in the young growth of twigs on young trees.

Larva in blueberries. In New Jersey, the larva of *C. packardi* commonly infests the early, immature fruits of cultivated blueberries (Lipman, Tomlinson), but it varies in importance from field to field and year to year. The larvae feed in several berries in the cluster before

maturing, so that only a few worms may destroy many berries. Vergeer informs us that they spin the berries together when they move from one to another. He notes further that they occasionally make holes to the outside of the fruit in addition to that by which they enter, but keep only one open, covering the others with silk spun transversely over the opening. The newly hatched larva eats into the fruit through a small hole difficult to detect. The location of these "pinprick" holes indicates that "the great majority of larvae enter the berries on the sides nearer the calyx than the stem end. Some enter the calyx next to the sepals."

Larva in cherries. As described by Hoerner and List (1952), the entrance holes made by the newly hatched larvae into the fruit of cherry are "very minute and usually have a small amount of frass present around the opening. The larvae tunnel through fruit around the stone." As Downes (1929, 1929a) expressed it, the larva bores into the fruit and mines between the flesh and pit of the cherry. He found the native host in British Columbia to be wild cherry.

Larva in rose. Forbes (1924) reported that the larvae of the "spring brood" bore into the buds of roses and blast them. This appears to be the first observation of the larva in rose buds. Heinrich (1926) names rose "tips" as one of the larval food plants. Since I found numerous larvae in the buds and hips of various wild roses, I conclude that rose is evidently another of the native American host plants.

In east central Illinois, the yearly development of *C. packardi* involves both the buds and hips. No less than two generations are produced here, the first or spring cycle predominantly in the buds, the last largely in the hips.

Larva in rose buds. The behavior of the larvae in relation to rose buds was observed many times, particularly at Urbana. Upon hatching from embryos that developed on the neck of the incipient hip, the small larvae entered the lamina of the buds in one of two places—at the neck or at the side of the bud itself. In a random sample, 70 larvae had entered by way of the neck, and seven bored in through the sides, usually in the basal two-thirds of the bud. When entering at the sides, they sometimes penetrated only the corolla exposed between the sepals, and less frequently perforated both sepal and the underlying petals. The initial entrance is oval and about 1.0 mm. in diameter but is enlarged for subsequent exit of the mature larva.

Buds inhabited for a day or more by the larvae are readily and reliably identified by the small mass of pale brown to black fecal frass that accumulates externally at the entrance. While some of the feces is expelled through the aperture to the outside, the bulk of it produced during larval development is deposited in the lumen of the bud.

The rose bud constitutes a nearly ideal situation for the development of the larva. It affords darkness which this evidently negatively phototropic larva requires, and a diversity of food material in the form of floral structures. This bud lumen also is the place where the larva molts. Especially the discarded head capsules may be found mingled with the silk-bound vegetable and fecal frass, those of the first instar sometimes lying at the entrance to the neck of the hip.

Usually the larva is found lying curled on the floor of the bud within the circular space between the mass of short pistillary tubes and the bases of the filaments and petals. In this position, the mandibles can readily reach the bases of the stamens and corolla, which parts constitute much of the food. The pistils, a clump of short, threadlike structures, seem not to suffer extensive, if any, attack. The pollen from the anthers is ingested in large amounts, for the digestive tract is often packed with yellow particles. Pollen may become available to the larva when the anthers fall to the bottom of the bud lumen after the filaments are severed.

In this connection, it is of interest that the larva appears sometimes, inadvertently, to perform the role of pollinator. In several instances, I discovered that the hip contained normal numbers of achenes despite the fact that larvae had severed the corolla from the receptacle and prevented its unfolding so, as a consequence, the anthers were not available to the usual external pollinating agents. The larva may chance to effect pollination when it chews off the filaments of the stamens whose anthers then fall upon the pistils.

Rose bud damage varies both in rate and kind; up to 65 per cent were found infested at Urbana. Small larvae that migrate to other buds while still immature cause little damage to the buds first occupied. In other cases, when the larva severs only some of the petals, the flower opens but has an asymmetrical shape. Often destruction is complete, as when all the petals are cut at their bases from the receptacle. The corolla then retains its normal conical shape and remains insecurely attached to the incipient hip, but turns gradually from the normal living red to dull red to dry brown, shrinking as it dries, and eventually falls off. Such dry conical buds are easily lifted intact from the hip.

Migration of larvae from bud to bud, or bud to hip, is probably not infrequent, even though one rarely discovers the larva in the act. Indirect evidence of such movements is often seen. I have found numbers of buds with small entrance holes but meager injury typical of this species, which can mean only that the inhabitant was small and had migrated elsewhere. Again, a bud may be inhabited by an advanced larva, which had fed but little and had deposited only little excrement, a circumstance indicating recent advent of the larva and its earlier growth in another bud.

In one such case, the larva was 8.0 mm. long and pink, submature, and little excrement occurred with it.

Larva in hips. In late June and early July, when budding and flowering are at an end, the larva invades the rose hip, which has now attained various sizes up to full-grown, yet is hard and unripe. I believe that some of the earliest inhabitants of the hips may be migrant, partly grown larvae that initiated their development in buds. But the prevalence of small larvae in the area of the neck and shoulder of hips shows that the majority of the larvae found in hips during July originated directly from eggs laid there. Commonly small larvae are found in incipient burrows at the equator of the hip, perhaps having entered between two hips hanging in contact. A small number occurs in the thick basal or petiolar end where they probably enter via the concavity around the stem. A few larvae gain entrance into the hypanthium through egg pits prepared by *Rhag. basiola*.

When inhabiting hips, the larvae of *C. packardi* are almost always confined to the hypanthium. Although usually residing so deep as not to be visible externally, some larvae bore along just beneath the skin so that the pattern of the burrow can be traced from outside. Rarely the larger larvae had eaten through the floor of the hypanthium, and some fecal matter lay on the exposed achenes. However, the achenes were not eaten. Such exceptional cases were discovered, mostly in the hips of *Rosa carolina*, and seem to occur in hypanthia so shallow that pressure of the ceiling of the burrow on the dorsum of the larva may have stimulated it to chew into the floor in order to gain space requisite to its life and avoid exposure to light.

The passages made through the flesh of the hip by the smaller larvae are narrow, nearly cylindrical tunnels. Their diameter increases gradually as each instar develops, but enlarges abruptly as the borer molts between instars. At some point in the more advanced phase of the larval stage the burrow is broadened without corresponding elongation. This the larva does by feeding at the lateral edges of the passage, thereby producing a broad, somewhat rounded blotch or mine. Superficially these cavities are recognizable by the dark color of the overlying hip skin, and closely resemble the dark blotches made by the advanced larvae of *Rhag. basiola*, but are readily distinguishable from the latter by their content of pellet-like excrement. That of the maggot is a homogeneous, semifluid brown paste. Moreover, the cavities of *packardi* are usually provided with one to three small apertures in the skin above the runways, the small first one at least being usually plugged with fecal pellets. Disposal of the excrement, by expelling it through the holes, is apparently practiced to some extent also by submature larvae, as is shown by the large heaps of fresh fecal pellets frequently seen in hip jars. How-

ever, much waste is voided directly into the burrow, for the older sectors of mines still inhabited, and deserted ones as well, are packed with excrement. The inhabited sectors of mines are devoid of feces and remain clean. When first eliminated, the pellets are rich reddish brown, but later turn dark brown to black, and then also are commonly overgrown with the mycelia of a fungus and apparently bound with silk.

The pattern or design of the system of burrows made by the larvae in the hips seems to assume various forms. However, this variety may be more apparent than real, so one asks whether there may be a single basic design. Perhaps, were the observer to note carefully the position of the hip on the rose bush, and then consider the design from that viewpoint, he might discover that the direction of the cavities with reference to the position of the hip bears a constant relation. Several factors, such as the direction of the sunlight, the pull of gravity, and the texture and odor, bitterness or sweetness of the hypanthium may be found to combine to produce the pattern. It is perhaps such complexity of interacting stimuli on insects that accounts for the inconclusiveness of our knowledge in the area of insect behavior.

Oral excretions. Mature emerged larvae sometimes emit sizable amounts of heavy, reddish brown fluid through the mouth when disturbed. It appears that the larvae concerned had fed on decomposing hypanthium in their final days in the hip. When irritated with a needle, the larvae produced small quantities of the fluid at each of several successive stimulations. The principal interest in these cases lies in the observation that the amount of dark substance present in the fore part of the digestive tract lessened visibly at each stimulation, proving that the substance originated in this tract, and not in the salivary glands. The contents of the glands are white and of small volume in the full-grown larvae of *C. packardi*.

Hibernation. Investigators are in general agreement that, whatever the host plant is, the cherry fruitworm spends the winter as a mature larva. Upon leaving the fruit or branch in which it develops, the larva constructs a protective hibernaculum, whose composition and location are subject to some variation, as is indicated by the following notes from the original literary sources.

Sanderson (1900) observed the larvae to winter in burrows in the "terminals" of apple. Their presence is often indicated by a leaf petiole remaining on the tip of a twig, the larval cell being present at the base of the petiole. Occasionally a case is formed on the trunk or branch of a tree. Hibernacula were composed of silk covered with bits of bark and dirt.

Downes (1929) reported that the mature larvae leave cherries to

search for a winter place and bore into dry twigs or bark to a depth of one to 1.5 inches. Stubs of pruned branches are preferred. Breakey and Webster (1939) stated the species hibernates in the stubs of twigs of sour cherry. Since they found no hibernating pupae, they deduced that the larva alone passes the winter.

Also in Colorado, where Hoerner and List (1952) observed the species, the full-grown larvae find winter shelter in the pruned twigs of cherry, under the bark, in the stems of weeds or grasses or in the ground. In the pruned stubs they tunnel the pith to a depth of 0.5 to 1.25 inches. They then line the excavated cavities with silk, and plug the opening where they remain through the winter. Dever (1953), in his work in Wisconsin, found that the mature larvae pass the winter, constructing their winter quarters by spinning a nest under a piece of loose bark, in a roughened stub of a broken branch or twig, or they may bore into the stubs of pruned branches. "It appears that any crevice, bark curl, or similar depression which will serve for protection of the overwintering larvae are utilized." The hibernacula have a light gray silken cover. This is easily removed, and then reveals two additional layers, which are very black, quite tough and brittle.

Describing the wintering of the cherry fruitworm with reference to blueberry, Vergeer (1954) states the larvae wander about on the bushes and commonly enter the pith of pruned twigs, tunneling as much as two inches, but usually less. "The opening in the end is closed smoothly and tightly with silk so that it normally escapes observation. They also encase themselves in cracks of the bark lower down on the bushes or even in plain sight on the outside of twigs."

Some mature larvae from rose wintered successfully in jars, where they spun their cocoons among hips or under the cloth covers on the jars. The observed high rate of winter mortality could, in view of the above reports, probably have been avoided by providing plant stems for the larvae to enter.

Pupation. After wintering in the hibernacula described above, the mature larvae of *C. packardi* transform through the pupal to the adult form. The particulars of the process of transformation have not been made known. The dates and duration of pupation are given in the following section.

Life cycle. According to published statements, the number of generations that develop in a year varies from one to three, or four. The reports from British Columbia (Downes), western Washington (Breakey and Webster), Door County, Wisconsin (Dever), and Grand Junction, Michigan (Vergeer), and my observations in northeastern Minnesota and northwestern Wisconsin, show that the species undergoes its life cycle

once per year in these areas. According to Hoerner and List, there is ordinarily one generation in a year in cherries in northern Colorado, but they found indications that a partial second occurred in 1946. Forbes (1924) reported three "broods" for New York, these appearing in May, June, and August, the "spring brood boring into buds of rose and blasting them; the later broods normally feed on the leaves. Similar habits on apple and peach" (Forbes). Sanderson (1900) gives data which seem to him to indicate four "broods" in a year in Delaware. The time data which I obtained from dissections of immature larvae from hips and rearing mature larvae and moths, strongly indicate there are two generations yearly at Urbana, Illinois, and vicinity.

One generation per year. In British Columbia (Downes), pupation occurred during the second week of May, when the transformation of a series of individuals required an average of 42 days. The adults emerged from late May to mid-June. In 1929, the height of emergence was reached on June 23 to 24. In Door County, Wisconsin, pupation took place "in the spring," and adults were trapped from July 6 to 26, 1950; June 12 to July 1, 1951; and June 9 to 18, 1952 (Dever). The adults therefore begin to appear there two to four weeks after the cherry petals fall, and continue for 14 to 21 days. Pupae were not uncommonly seen projecting from the hibernacula just before and after the emergence of the adults.

At Grand Junction, Michigan, the overwintered larvae pupated early the next May in the hibernacula, and the adults emerged over a six-week period that began during the last week of May, but did so mostly during the first three weeks (Vergeer). In Colorado (Hoerner and List), the wintered larvae pupate the following May, the average duration of the pupal stage there being 29 days. As determined by the use of bait traps, the first moths appeared near the first of June. In 1947 and 1949, the peak of emergence was on June 15, and in 1948 it was reached on June 7. Moths were captured as early as May 17 and as late as July 7 in northern Colorado.

In British Columbia, eggs were laid as early as June 15 in 1927, and the first ones on June 24, 1929. Incubation required 10 to 11 days, and the resulting larvae reached maturity in about 30 days (Downes). In Colorado, eggs were readily found during the second half of June in heavily infested cherry orchards. Under laboratory conditions, a few eggs hatched in seven days. In an average season, practically all the larvae have left the fruits by the time the crop is harvested in the latter half of July (Hoerner and List). Dever found that the larvae in cherries complete their development in about three weeks, and that some individuals attack several fruits before they become full-grown. His work in the years 1950 to 1952 showed the larvae sometimes mature and leave the fruit before cherry harvest in late July to early August, but in other

years, some still remained in the ripe fruits. Near Fruitport, Michigan, Vergeer examined 207 blueberries which bore evident damage by insects on July 8, 1953, and found only one such berry that still contained a cherry fruitworm. He states in effect that the larvae become full-grown toward the end of June and the first part of July, and do not develop beyond this condition until the following spring; i.e., they undergo a prolonged diapause.

Although buds and flowers of *Rosa acicularis* and *blanda* were still present in July in northeastern Minnesota, my notes contain no mention of larvae found in buds. Dissection of unripe hips produced the first larvae on July 21; these were small, 2.0 to 3.0 mm. long. Examination of sample hips at intervals during the months of August and early September in 1945 to 1951 revealed larvae varying greatly from first to last instars, and showed also that some had already matured and emerged from the hips by mid-August. Samples of ripening hips from Eaglesnest, kept in jars, yielded mature larvae up to October 15 at Urbana. These records indicate that *C. packardi* in rose hips begins its larval life in the first half of July, and that full-grown larvae appear from mid-August to mid-October to enter their winter diapause.

All the lots of hips which originated in northwestern Wisconsin were picked and placed in jars at Urbana during the first third of September, 1945 to 1951. Some full-grown larvae issued within a day after the hips were picked, showing that emergence, particularly at Chetek where the majority of hips was obtained, began in August. Emergence continued into October from four of the five annual samples, and, in the extreme instance, to October 28, 1946. Larvae emerged as late as November 2 and 5, 1947, from hips taken at Madison and Black River Falls, Wisconsin, respectively.

Two generations per year. In east central Illinois, *Cydia packardi* completes its life cycle twice in a year, the first largely in rose buds, the second in rose hips. This fact is clearly indicated by the dates of emergence of the adult moth and the times of occurrence of the early and late, or extreme, instars.

Adults, which developed from mature larvae in captivity, emerged at two distinct seasons of the year, namely May 3 to 28, and June 29 to July 29. My data show that the maturity and emergence of larvae from rose buds and hips occurred about June 5 to mid-July, and again between August 22 and December 8. I do not pretend to assign the larvae of July 7 to August 16 as to generation; they may have been late members of the first generation or early comers of the second, for there is doubtlessly some overlapping in the larval stage of the two cycles. Early instars appeared in two distinct time periods. The first to third instars predominated numerically from June 5 to 20 and again from July

7 to August 16. The low incidence of larvae in hips on June 27 to July 6 indicates this was the preovipositional and ovipositional interval between generations. The seasons of the embryonic and pupal stages may be approximated by inference from the dates of larval and adult stages. Pupation occurs in late April forward, and during parts of June and July; oviposition largely in May and July.

PARASITES OF *Cydia packardi*

The following parasitic Hymenoptera have been reported in the literature. In Delaware, the hibernating larvae of *C. packardi* were parasitized, probably to the extent of 50 per cent, by the braconid, *Bracon mellitor* Say (Sanderson, 1900). List (1932) reared the chalcid, *Eurytoma tylodermatis* Ashm. from the larva in Colorado, and Putnam (1935) reported the chalcid, *Psychophagus omnivorus* Walk., a braconid, *Ascogaster carpocapsae* Vier., and an ichneumonid, *Glypta rufiscutellaris* Cress. from this host in Ontario. About one per cent of the cherry fruit-worms collected by Hoerner and List (1952) in 1948 were parasitized, mostly by *Ascogaster quadridentatus* Wesm., a few by a species of "Bassus." Driggers (1932) found that chalcids of the genera *Eurytoma* and *Eupelmus* were apparently hyperparasites of *G. rufiscutellaris* in the cocoons of *Cydia molesta* (Busck) in New Jersey.

I have discovered several species of hymenopterous parasites and two genera of clerid beetles attacking the larva of *C. packardi* in rose buds and hips. My observations, combined with information from the literature, are given below for these species.

Glypta rufiscutellaris Cress., Ichneumonidae, Hymenoptera

This native North American parasite was investigated extensively between 1925 and 1945 as a result of the discovery that it constituted somewhat of a check on the newly introduced oriental fruit moth, *Cydia molesta*. The principal contributions pertaining to its immature stages and bionomics are by A. W. Crawford (1933) and Montgomery (1935).

Glypta rufiscutellaris (Figs. 28, 29-32) was named and first described by E. T. Cresson in 1870 from specimens of both sexes which originated in Connecticut, New Jersey and Illinois. The original description states that the rufous scutellum and the black mouth readily distinguish it from its relatives.

Distribution and hosts. *G. rufiscutellaris* occurs from the Atlantic Ocean west to Alberta, Canada, and to Utah, in the Transitional and Upper Austral faunal zones (Muesebeck, et al., 1951). I have found it present in all the main areas in which the insects of rose hips were in-

vestigated, as follows: Eaglesnest, Minnesota, north shore of Lake Superior between Little Marais and Grand Marais, Minnesota; Solon Springs, Gordon, Rice Lake, Chetek, Endeavor, and Madison, Wisconsin; at several rose stations in Urbana, at Mayview and Philo, and at Velma (near Taylorville), all in Illinois.

The members of the braconid subfamily Banchinae, which includes the genus *Glypta*, are internal parasites of caterpillars (Muesebeck, et al., 1951). *G. rufiscutellaris* appears to select small lepidopterous hosts which live enclosed in such parts of plants as fruits, slender stems, husks on nuts, and leaf rolls, where penetration of the protective plant wall by the ovipositor is necessary to reach the host within.

A native host frequently reported for *rufiscutellaris* is the ragweed borer, *Epiblema strenuana* Wlk. in the stems of *Ambrosia artemisiifolia* L. The adult has been reared from this host at St. Davids in the Niagara fruitbelt of Ontario (Putnam, 1935; van Steenburgh, 1934; Boyce, 1946), in Connecticut (Friend, 1942), western New York (Daniel, 1930), New Jersey (Driggers, 1930), Delaware (Rice, 1935), Virginia (Bobb, 1939), Ohio (Stearns and Neiswander, 1930; Blackburn, 1944) and Indiana (Montgomery, 1933). Bobb reared it also from *Epiblema otiosana* Clem. in *Bidens bipinnata* L. and *Xanthium canadense* Mill. in Virginia. Investigators have found the ragweed borer to be a valuable alternate host of *rufiscutellaris* as a factor in the control of the oriental fruit moth. For this reason, several eastern entomologists have advocated that the ragweed be permitted to grow in and near peach orchards.

Other native hosts of *G. rufiscutellaris* recorded to date are: *Laspeyresia caryana* Fitch in the husks of *Carya ovata* (Mill.) K. Koch (Putnam, 1935); the lesser apple worm, *Grapholitha prunivora* Walsh (Putnam, 1935); *Cydia* (*Graph.*) *packardi* in the fruit of cultivated red cherry (Putnam, 1935); *Argyrotoxa semipurpurana* Kearft. on *Quercus rubra* L. and *Q. coccinea* Muench. (Putnam, 1935). All these records by Putnam pertain to St. Davids, Ontario. Putnam (1938) adds other native hosts of *G. rufiscutellaris* in Ontario as follows: *Epiblema scudderiana* (Clem.), a gall-former on stems of goldenrod; *Epiblema obfuscana* Dyar, boring in stems of goldenrod; *Melissopus latiferreanus* Whshm., in acorns of red oak, and a leaftier on *Crataegus* L., tentatively identified as *Epinotia laracana* Kearft. Garman (1930) reared this *Glypta* from the strawberry leaf roller, *Ancylis comptana* Froel., in Connecticut. From *Polyochrosis carduana* Busck, Blackburn (1944) obtained small numbers of it that bored in the tips of thistle in Ottawa County, Ohio, and he also obtained it from the goldenrod gall moth, *Gnorimoschema gallaesolidaginis* (Riley). In California, Mackie (1944) found that the potato tuber moth, *Gnor. operculella* (Zell.) was useful as a host for rearing this parasite. In Washington, Oregon, and western California, Dohanian (1942)

discovered it attacking the filbert worm, *Cydia (Mellisopus) latiferreana* (Wlsm.) in hazelnuts (*Corylus*).

Additional hosts of *G. rufiscutellaris* are named in the Synoptic Catalog (Muesebeck, et al., 1951), whose original literary sources I have not unearthed. These are the codling moth, *Carpocapsa pomonella* (L.), and *Proteotera aesculana* Riley. I have several times obtained *Glypta rufiscutellaris* from Illinois, Wisconsin and Minnesota, as a parasite of *Cydia packardi* in the buds and hips of roses.

Also many rearing records of *G. rufiscutellaris* relate to the oriental fruit moth, *Cydia molesta*, as a host, and usually it is rated as second only to the imported braconid, *Macrocentrus ancylivorus* Rohwer as a natural check on this pest. In this relationship, it is known both from the Niagara peninsula and the southwestern area of Ontario, where peach is grown (Boyce, 1946). It is regarded as significant also in Maryland (McConnell, 1932), New Jersey (Driggers, 1940), Delaware (Haden, 1935), Pennsylvania (Anon., 1934), western New York (A. W. Crawford, 1933), Virginia (Bobb, 1939), Ohio (Stearns and Neiswander, 1930), Michigan (Merritt, 1933, 1933a) and Missouri (Wingo, 1940). Butler (1933) reared a few individuals from *C. molesta* in Rome County, Tennessee. Six colonies of this parasite were liberated by agents of the Bureau of Entomology, U.S. Department of Agriculture, in peach orchards in Georgia and the Carolinas (Marlatt, 1931). It has also been exported from the United States to foreign countries, including Japan (Ishii, 1940), Goulburn Valley, Victoria, Australia (Anon., 1938), Uruguay (Lepage and Fadigas), and Italy (Grandi).

Adult. Females 5.0 to 6.6 mm. long, males 4.6 to 5.8 mm.; form slender, the males more so; body predominantly dark brown or black; mesonotum and thoracic pleura more or less reddish brown to rufous, the notum sometimes almost black; antennae and sheaths of ovipositor brown, the sheaths 3.5 to 4.4 mm. long; legs mostly light brown, fore coxae white, fore and middle tibiae paler than femora, the hind tibiae white except the apical thirds black; fore tarsi uniformly light brown; hind tarsi black with white bands, mid tarsi same, but paler. Abdomen beneath whitish, membranous and concave; ovipositor sheath about as long as the abdomen (Fig. 28).

Fed a combination of sugar and water, the adults can live for a month or more in cages. The males are sexually active upon emerging from the cocoons, and mating takes place at once under favorable conditions. A. W. Crawford (1933) described the activity of mating. Parthenogenetic reproduction has been reported by three observers. Montgomery (1935) found larvae of *Glypta* in a few oriental fruitworms which had been exposed only to virgins. Putnam (1938) reported an unmated female which parasitized newly hatched fruitworms, in which 12 males then

developed. Also Crawford learned that uninseminated females will oviposit and the embryos develop normally. In all cases, the progeny was male. These, when mated with virgins, produced offspring of both sexes.

Oviposition. Each ovary of *Glypta* consists of 22 to 28 ovarioles of the meroistic type (A. W. Crawford, 1933). The grown eggs remain in the lower chambers of the tubes until deposited. As many as 86 fully developed eggs occurred in a single female. Oviposition begins within 2 to 6 days after emergence from the cocoon. The maximum deposition was secured at 70 to 80° F. and when the larvae of the peach moth were made available in the morning or late afternoon. The female was incited to oviposit only when frass or silken webbing of the host larva was present at the entrance to the burrow. These materials, rather than the larva itself, appear to trigger the egg-laying response. The host was attacked only when concealed within its burrow.

The first indication that oviposition is about to occur is the rapid movement of the antennae as the female starts feeling over the twig in an effort to locate the point of entrance of the host larva. Upon finding this hole, the female prods into it with the ovipositor. The instant the terebra comes into contact with the host larva, she immediately ceases all movements of the body for 15 to 25 seconds. She then withdraws the terebra and usually crawls down the twig, wiping the head and antennae with the fore legs. However, sometimes a second egg may be laid in the same larva before the female leaves the twig, or, in other cases, she may return after a brief absence for a second oviposition. From a number of timed depositions, the average duration of the process was found to be 19 seconds.

Eggs are laid singly, and placed free in the body cavity close to, but never in, the digestive tract, and never in the fat body or muscles. The newly laid egg measured 0.300 to 0.308 mm. long, and 0.090 to 0.1125 mm. wide at the broadest, or cephalic, end. It is slightly curved, and the caudal part more broadly rounded. The thick chorion gives the egg a somewhat solid appearance (Fig. 32). Embryogenesis requires about 41 hours at 75 to 80° F. (Crawford).

Reaction of host to attack. The response of the oriental fruitworm subjected to attack by female *Glypta* depends, according to Crawford (1933), largely on the depth of the larval burrow in the peach twig. When the larva inhabits a burrow so short that it cannot retreat, it emerges and crawls rapidly away, unless the parasite holds it with her antennae until she places an egg into it. If the burrow is longer than the ovipositor, the larva retreats hastily into it as a means of escaping attack. But if the burrow is intermediate in depth so that neither of the above responses is possible, the larva is liable to a number of thrusts with the terebra. It appears that the host is not paralyzed by the attack,

for Crawford observed the larva is strong and natural in its movements thereafter.

Larval life. The oriental fruitworm may be parasitized in any of the instars, from the first to the last. However, if one-day-old larvae are attacked by the female *Glypta*, very few parasites reach maturity. Again, if eggs are inserted into late third instars, the parasite fails also, for the reason that the host completes its larval development long before the parasite becomes full-grown, and the large majority of the hosts pupated. Almost 100 per cent survival of the parasites was obtained with host larvae of the late first and early second instars (Crawford). Also Montgomery (1935) secured best results in the form of adult *Glypta* with young larvae of *Cydia molesta*. Larvae approximately 24 hours old when exposed to ovipositing *Glypta* showed parasitization of 80 per cent, whereas larvae two days old when so exposed, showed 53 per cent, and larvae four days old, only 16 per cent.

I have seen only the first two instars of *G. rufiscutellaris* in larvae of *Cydia packardi* (Figs. 30, 31). Both Crawford and Montgomery describe and figure four instars. These are similar in being cylindrical in form. The first instar is distinct in having a pale brown, moderately sclerotized head capsule. When newly hatched, the parasite is 0.52 mm. long and 0.11 mm. wide; the full-fed fourth instar varies from 5.0 to 6.98 mm. in length by 1.5 to 1.98 mm. in width. All the instars bear a short caudal process, which becomes shorter and shorter from the first to the fourth instar. Exclusive of this process, all the instars have 13 postcephalic segments. The first three instars lack spiracles, the fourth has them visibly developed (Crawford, Montgomery).

Throughout the course of growth of the instars, the larva of *Glypta rufiscutellaris* appeared to be free in the body cavity of the oriental fruitworm (Montgomery, 1935). The host's viscera became crowded against the body wall as the parasites grew. The fourth instar then consumed the tissues of the host, and the full-grown parasite filled the host skin to distension. Finally the head of the mature parasite larva appeared through the host's cuticle. Montgomery states the head emerged through the dorsa of the last segments of the host larva. Crawford observed that the opening was made either in the anterior or posterior end, depending on the direction the emergence-ready larva had last headed in the host. Both these investigators saw that the old host skin is worked off by vigorous wriggling or contortions of the parasite. To expedite this process, the parasite may even bend the head around to the tip of the abdomen. As Crawford also pointed out, the escape of the full-grown parasite larva from the host skin is therefore a process of shedding rather than emergence.

Cocoon, prepupa, and pupa. Having discarded the host skin, the full-grown larva of *Glypta* encloses itself by spinning its cocoon of white silk. The cocoon "has the appearance of a transparent silken membrane when completed and has an average measurement of 10 mm. by 35 mm." (A. W. Crawford). In three to four days after shedding the host skin, the parasite has transformed to a pupa. I presume this statement applies only to the summer generation, since the other winters as mature larvae. Half of the three to four days is spent as a prepupa. Crawford's figure indicates that the prepupa resembles the larva in general form, but has the dark pupal eyes visible through the cuticle. At first white, with reddish eyes, the pupa grows darker as it develops, assuming the color of the adult as it does so. The female pupae average 7.9 mm. long by 2.02 mm. wide. The males are slightly smaller.

Superparasitism. Montgomery (1935) found an egg and a first instar of *G. rufiscutellaris* in one larva of *Cydia molesta*. I discovered two instances of duplication in *C. packardi*. In one instance, two eggs were found in a caterpillar of this moth; in the other, two living immature larvae occurred together in one host.

Life cycles. The number of cycles or generations completed by *Glypta rufiscutellaris* varies from one and a partial second to three in a year, according to reports published to date. Stearns and Neiswander (1930) believed it to be "two-brooded" in northern Ohio in 1927 to 1929. There is evidence of two generations at St. Davids, Ontario (Putnam, 1938). In 1934, the adults of the first generation had already emerged there before May 14, when the first collection of the host, *Epiblema strenuana* Wlk. in ragweed, was made. In 1935, adults appeared from the same host from May 8 to 24, and in 1936, from May 4 to 14. Adults of the second generation issued through August 8 to 18, 1932, and August 1 to September 10 in 1934. A. W. Crawford (1933) reported one and a partial second generation from *E. strenuana* in western New York. Adults of the spring "brood" emerged between June 10 and July 22, 1931; those of the partial second, between August 12 and 28, 1931. But when attacking *Cydia molesta*, which completes three cycles in a year in New York, *Glypta* undergoes its life cycle three times yearly, one for each generation of the host (Crawford). Timewise, these were found to be distributed as follows: full-grown larvae of the first generation are in their cocoons about the latter part of June and the first part of July; the full-grown larvae of the second are in their cocoons in latter July and during August; those of the third cycle occur there about the middle of September. Crawford found that the emergence of the adults of the three generations began as follows: first generation, July 2, 1931, and July 7, 1932; second, August 8, 1931, and 1932; third, September 22, 1931, and

September 30, 1932. Males began to appear before the females in both these years.

My rearings of adult *Glypta* from *Cydia packardi* indicate two cycles per year in eastern Illinois. Of the 43 adults obtained from hip jars, some emerged between June 19 and July 17, whereas others appeared in August and September. A quantity of hips from San Jose, Illinois, yielded 29 adults from late September to October 27.

That *Glypta rufiscutellaris* winters as a mature larva is indicated by all reports. Driggers (1930) stated that the winter is passed in New Jersey by the full-grown larva in its own cocoon which lies within that of the host. Crawford (1933) wrote that the parasite exists as a full-grown larva within its cocoon until the middle of the winter, then develops to a prepupa, with eyes, and continues as such until the first part of April. Also the report of Putnam, for Ontario, indicates the species winters as a full-grown larva in the host's cocoon in the host plant. The fact that McConnell (1928) in Maryland, and other investigators in eastern United States, reared adult *Glypta* from overwintered oriental fruitworms, indicates that the parasite winters in some immature stage.

At temperatures ranging between 75 and 80° F., embryogenesis averaged 35 hours. The four instars required 5 to 6 days, 3 to 4 days, 4 to 5 days and one to 2 days, respectively. The prepupal form is retained about 2 days, and is terminated by the molt that discloses the pupa. The average survival of adult males of three generations was 19.6, 16.5 and 20.7 days; of females, 28.4, 28.2 and 31.9 days, respectively (Crawford, 1933). When kept at high humidities, the average lifetime of male *Glypta* was 30.69 days; of females, 49.43 days (Rice, 1935).

Ascogaster sp.?, Braconidae, Hymenoptera

That my series of 51 first instars dissected from the larvae of *Cydia packardi* in rose hips represents a species of *Ascogaster* is indicated by several records, as follows. I obtained one adult of an undetermined species of this genus from a jar of hips inhabited by this caterpillar. Putnam (1935) reared *A. carpocapsae* Vier. from the cherry fruitworm in Ontario; Hoerner and List (1952) had *A. quadridentatus* Wesm. from this host in cherry in Colorado. The most convincing evidence that my 51 first instars probably are a species of *Ascogaster* lies in the very close structural similarity between them (Fig. 46) and Cameron's (1938) drawing of the first instar of *A. quadridentatus* from *Cydia nigricana* Steph. Also my observations on the bionomic features of these instars agree with the accounts given by Cameron (1938) and by Rosenberg (1934), who investigated the parasites of *Cydia pomonella* L. in France.

The first instar is easily distinguished from all other parasitic larvae

found to date in insect hosts developing in rose hips. When newly dissected from the host, the parasites varied from 0.6 to 1.9 mm. in length, and were about one-fifth as wide; sides subparallel; body decidedly depressed, flat above, form varying from straight to sinuous as viewed from above, smooth with no obvious vestiture.

Head pale brown, sclerotized, subquadrate as seen from above, tending to bulge at the sides behind; mouth parts obscure, protruding slightly from the middle of the anterior margin of the head. Postcephalic parts white, the several segments uniform in size and shape, each protruding prominently and roundly at the sides. Abdomen terminates in a short but distinct, broadly rounded vesicle narrower than preceding segments (Fig. 46). The thorax, abdomen and caudal vesicle constitute 13 segments. When left in water only a few minutes, the body swells so that the segments, and particularly the caudal ones, tend to lose their form and identity, and even the head assumes an unnatural distended form. Usually the newly exposed larvae lie straight in the water in the dissecting dish. When absorbing water, they may assume a sinuous form.

My series of 51 first instars was obtained in the course of dissecting larvae of *Cydia packardi* from the hips of *Rosa acicularis*, *blanda*, *carolina*, *palustris* and a *Rosa* sp. in the years 1946 to 1951. The parasite occurred at Eaglesnest, Minnesota; Chetek, Wisconsin; Jamestown, Indiana; Taylorville and Mahomet, Illinois, and West Alexandria, Ohio. Nine individuals of the series were discovered between August 7 and 19, at Eaglesnest, in the larvae of *C. packardi* one-half to two-thirds grown and therefore still feeding in the hips. These parasites were 0.6 and 0.7 mm. long. The remaining 42 were contained in mature host larvae which had issued from the hips. These parasites had grown to 1.75 to 1.9 mm., but still had not developed beyond the first instar. These were dissected out of the hosts between August 29 and November 15. That they remained as first instars so late as mid-November strongly indicates the parasite winters as the first instar, in the normally overwintering mature larva of *C. packardi*. Accordingly the first instar, after a prolonged slow growth to its advanced, mature state, seems to enter into diapause which may terminate in late spring or early summer of the ensuing year.

Rosenberg (1934) and Cameron (1938) found that the mature first instar of *A. quadridentatus* in *Cydia pomonella* and *C. nigricana* go into diapause that persists through the winter in the mature host larva. They found also that the females insert their eggs into the embryos of the host moths. Many species of practically all microlepidoptera of habits similar to *C. packardi* are parasitized by *A. quadridentatus*, according to the above investigators.

The Long-Tailed Parasite. Hymenoptera

Specific identification of this endoparasite of the larval *Cydia packardi* has not been made because only the first instar is known to me. The common descriptive designation employed above is, of course, provisional.

This first instar (Fig. 50) is structurally unique among parasites obtained from hosts in rose hips in being extremely slender, with a tapering caudal process that is almost as long as the head, thorax and abdomen combined. Head longer than thick, its venter provided with a blunt process; in some views it appears also to have on its venter a pair of minute, obscure, forked appendages which are directed caudoventrad; postcephalic part whitish, clear, subcylindrical, tapering moderately toward the caudal process; this latter single appendage is clear, broad at base, and narrows gradually to a fine point behind, normally moderately arched and directed almost straight caudad. The postcephalic area, exclusive of the caudal appendage, appears to comprise 12 segments, each of which is divided into an anterior and a posterior half by a superficial transverse constriction.

When newly removed from the host to water, the parasite reacts by rolling sidewise quickly and often, and bending the cephalic end stiffly ventrocaudad, whereby the body takes a J-shaped posture; or the cephalic end and the caudal process may be bent ventrad U-shaped, and again straightened alternately, while the "tail" flails about slowly.

Only six individuals of this form were discovered in the course of dissecting cherry fruitworms for parasites from 1945 to 1951. These were taken as follows:

Jamestown, Indiana, four. One measured 1.3 mm. long, from host one-third grown, October 2, 1945; two measured 1.8 and 2.0 mm., from mature, emerged hosts, October 19, 1947, and one which was 2.0 mm. long, from a mature, emerged host, October 31, 1947. All originated in hips of *Rosa palustris*.

Philo, Illinois; one parasite 2.0 mm. long, from a host about one-fourth grown, July 8, 1948, in hip of *Rosa carolina*.

Fox Ridge State Park, Charleston, Illinois; one parasite, 2.1 mm. long, from a host four-fifths grown, July 31, 1949, in hip of *Rosa virginiana*.

Because only first instars were discovered in the over-all period of July 8 to October 31, the species may prove to complete one generation in a year and undergo a prolonged diapause, including the winter season, as a first instar.

Scambus hispae (Harris), Ichneumonidae, Hymenoptera

The adults in my collection are slender, dark brown to black, the

males measuring about 4.7 mm. long, the females 5.0, with sheaths of the ovipositor 3.0 mm. long; coxae and femora brownish yellow; front legs to hind, the tibiae are white, to white, ringed with black.

This ichneumon has been treated in the literature under several scientific names. See the Synoptic Catalog by Muesebeck, et al., (1951, p. 187), for synonyms. This source states also that the species is trans-continental in the Canadian, Transitional and Upper Austral faunal zones of North America, and that "the species of *Scambus* are parasites of small Lepidoptera in buds, fruits, leaf rolls, leaf mines, galls, or similar retreats." *S. hispae* has been reared from thirty species of small Lepidoptera, not including *Cydia packardi*, and appears to be the most common member of the genus. It is a solitary ectoparasite.

My belief that *S. hispae* parasitizes *Cydia packardi* in rose hips is based on two kinds of evidence. First, I have obtained a series of adults from jars of rose hips in which the cherry fruitworm was the only lepidopteron present. Also, the published reports show that *hispae* parasitizes host caterpillars having habits similar to those of *packardi*. Second, in June, 1951, I picked a quantity of buds of *Rosa carolina* at Urbana that bore the unmistakable injuries made by larvae of *packardi*. On July 3, 1951, an adult male *hispae* appeared in the cage.

Also fourteen adults were reared at Urbana from quantities of rose hips stored in fruit jars, as follows:

Eaglesnest, Minnesota, one ♂, September 24, 1950; two ♂'s, September 12 and 13, 1951, and one ♀, September 22, 1951; one ♀, May 25, 1948, and one ♂, May 28, 1948. All these originated in hips of *Rosa acicularis*.

Solon Springs, Wisconsin, one (sex unknown), October 7, 1946; three ♂'s, October 6, 11, and 24, 1947. From *Rosa blanda*.

Rice Lake, Wisconsin, one ♂, October 8, 1947. From hips of *Rosa blanda* or *carolina*.

Chetek, Wisconsin, two ♂'s, October 5, 1949, September 22, 1951. From hips of *R. blanda* or *carolina*.

Urbana, Illinois, one ♂, July 3, 1951. From bud of *Rosa carolina*.

Only fragments of bionomic data appear in the literature, so far as I have seen it. Cushman (1927) observed it as a solitary ectoparasite on the larvae of the pine tip moth, *Rhyacionia frustrana* (Comst.). It attacks full-grown or large larvae, and its cocoon consists of a silken lining to the burrow of the host. He added that it is "a common parasite of internally feeding microlepidopterous larvae, with many known hosts." Doner (1936) found it (*Pimpla indagatrix* Cr.) parasitizing the mature larvae of *Coleophora pruniella* Cl. in Wisconsin. Under the name *Epiurus indagator* (Cr.), Porter and Garman (1923) reported *S. hispae* as one of the parasites reared in Connecticut from the European "apple and thorn

skeletonizer," *Anthophila (Hemerophila) pariana* (Clerck). It oviposits on the full-grown larva, and the adult emerges from the host cocoon. Brunson and Allen (1948) reported it as a "cocoon parasite" of *Cydia molesta* in New Jersey and other eastern states, and McConnell (1928) obtained adults from the overwintered larvae of *molesta* in Maryland. As observed by Coppel (1946) in British Columbia, it performed as a primary parasite of the spruce budworm, *Choristoneura (Archips) fumiferana* (Cl.), and wintered as a secondary in the cocoons of the ichneumonid *Phytodietus fumiferanae* Rohwer.

According to Schaffner and Griswold (1934), it (*Epiurus nigrifrons* Vier.) is a solitary parasite in New Hampshire and New Jersey where it hibernates in the host pupa and has at least two generations in the year on *Halisidota tessellaris* S. and A. and *Hemerocampa leucostigma* S. and A. On two occasions I reared *Scambus hispae* from hosts obtained in the vicinity of Urbana, Illinois. In both cases, the species was identified by R. A. Cushman, U.S. National Museum, as "*Epiurus indigator* Cress." In the first instance, adults emerged from the central cell of the gall made by the cynipid, *Disholcaspis mamma* (Cress.) and appeared to have parasitized the larva of this insect, but the host may have been some lepidopteron that entered the vacated gall to cocoon (Balduf, 1926). In the second instance, it attacked the common bagworm, *Thyridopteryx ephemeraeformis* (Haw.). Bags dissected in the early part of the period of March 31 to April 18, 1936, contained overwintered mature parasitic larvae in the chrysalises of both male and female hosts. Most bags contained one parasite, but a few had two larvae or cocoons in the chrysalids. The series of 16 adults reared that spring comprised 15 females and one male (Balduf, 1937).

Euderus cushmani (Crawford), Eulophidae, Hymenoptera

This chalcid shares the role of solitary ectoparasite on the larva of *Cydia packardi* with *Scambus hispae*. The recorded hosts, *Polyochrosis viteana* (Clem.), *Anarsia lineatella* Zell., *Argyresthia thuiella* (Pack.) and *Coleophora pruniella* Clem., as given in the Synoptic Catalog (Muesebeck, et al., 1951), are, like those of *S. hispae*, larvae of small Lepidoptera which live concealed in parts of their food plants. According to the same source, *E. cushmani* has previously been reported from Pennsylvania, Wisconsin and California. I have it from Wisconsin and Illinois.

J. C. Crawford (1915) described *E. cushmani* from specimens whose host was *Polyochrosis viteana*. My adults from *Cydia packardi* are dark, the males approximately 1.0 mm. long, the females about 2.0 mm. long. Kiefer and Jones (1933) reared *E. cushmani* (Crawf.) (*Secodella cushmani*) from the immature larvae of *Anarsia lineatella*, on which it ap-

parently was an ectoparasite. Adults appeared on July 21, 1932, and March 6 to 8, 1933, in California. I have obtained 10 adults, all of which emerged from hips stored in jars, as follows:

Chetek, Wisconsin, two ♀'s, September 13, 1951; three ♀'s, September 10 and 18, 1951, and one ♂, September 18, 1951. From hips of *Rosa carolina* or *blanda*.

Madison, Wisconsin, one ♀, September 2, 1946. From hips of *Rosa arkansana*.

Urbana, Illinois, one ♀, May 10, 1949. From hips of *Rosa palustris*. Also two ♂'s, August 16 and September 14, 1951, from hips of *R. carolina*.

The male secured at Urbana on August 16, 1951, developed from an advanced black pupa found in a mine of *Cydia packardi* in a rose hip on August 5. The host's burrow originated at the neck of the hip and extended to the equator, where the host had last fed and was overcome by the parasite. The pupa, adjacent to the remains of the host, was not encased in a cocoon. The small length and breadth of the burrow indicated that the host was very small when it was attacked by the female *Euderus*.

AN UNIDENTIFIED ECTOPARASITE OF *Cydia packardi*

At Eaglesnest, on August 25, 1947, I discovered an egg 1.9 mm. long (Fig. 51) adjacent to a limp submature larva of *C. packardi* in its mine in a hip of *Rosa acicularis*. The parasite—probably a large ichneumonid sp.—had killed the caterpillar with a paralyzing thrust of the terebra.

PREDATORS OF *Cydia packardi*

Enoclerus? sp. and *Phyllobaenus* sp., Cleridae, Coleoptera

Besides attack by the parasites discussed above, *Cydia packardi* is attacked occasionally by predators. From time to time since 1945, I have come upon coleopterous larvae either in the burrows or mines of the caterpillar in the hypanthia of rose hips, or free among hips stored in rearing jars. Mr. O. L. Cartwright of the U.S. National Museum examined some of my specimens and determined them as members of the genera *Phyllobaenus* and "probably *Enoclerus*," of the family Cleridae. I have compared the rest of my specimens with those determined by Cartwright and find all are identical with those he returned. Reference was made also to the work of Böving and Champlain (1920) on the larvae of this interesting family. The following descriptions pertain to what appear to be mature individuals, and will serve to distinguish the two generic types found in hips of roses.

Enoclerus? sp. Length, 9.0 mm.; body slender, its width approximately uniform throughout; numerous white bristles tend to be bunched on the

tergal and pleural aspects of the postcephalic segments, shorter ones over the venter; body whitish, except cerci or caudal processes, pronotum and all of head brown to reddish brown and sclerotized; cerci sturdy, straight, moderately divergent, their apices blunt except dorsocaudal angle of each member pointed.

Phyllobaenus sp. Length, 8.0 mm.; spindle-shaped; numerous white bristles distributed somewhat generally over the body; body mostly whitish or suffused with purple, except head which is medium brown, sclerotized, also pronotum brown back to the heavy, broadly V-shaped purple figure; a pair of small dark lunate marks on meso- and metanota, these nota also pale purplish; abdominal tergites 3, 4, 5 and 7 dark purple, and suranal plate dark brown; prosternum with a T-shaped purple design, venter of body otherwise light; coxae and femora ectally brown. No cerci of any sort present.

Three individuals of *Enoclerus*? sp. were obtained, as follows:

Mayview, Illinois, August 1, 1948. In an extensive mine of *C. packardi* in a hip of *Rosa carolina*, I found a head of the caterpillar, with shrunken postcephalic parts attached. The size of the head indicated the victim was nearly full-grown when attacked, from behind. In the same mine occurred a larva of *Enoclerus*? sp., about 6.0 mm. long, or two-thirds grown. The facts and circumstances here make it practically certain that *Enoclerus*? preyed on the larva of *C. packardi*.

Mayview, Illinois, August 9, 1948. A mine of *C. packardi* in a hip of *Rosa carolina* extended from neck to base of petiole, or a distance of 12 mm. The sizable dead caterpillar had been greatly reduced in volume, and the mine was occupied by a larva of *Enoclerus*? sp. 5.5 mm. long, and estimated to be two-thirds grown.

Velma, Illinois, October 14, 1945. The clerid larva, 10.0 mm. long, was moving over the bottom of a jar containing hips of *Rosa carolina*. When crawling, it progressed smoothly and without elevating any parts of the body. An anal proleg supported the end of the abdomen.

Five individuals of *Phyllobaenus* sp. were taken. All originated in extensive, mature stands of wild *Rosa carolina* growing in an area of shifting sand near San Jose, east of Havana, Illinois. They came to my notice between August 1 and October 25, 1951. The larva obtained on August 1 occupied a large mine of *C. packardi* that opened at the petiolar end of the hip. Since I failed to see the victimized caterpillar, I conclude it had been killed and largely consumed by the clerid larva, which was 5.5 mm. long. Its distended form indicated it had recently fed, or was about to molt.

The other four larvae of this genus had apparently become full-grown since they had emerged from the hips and were taken moving free among the hips in the jars. They measured 7.5 to 10.0 mm. in length.

These clerids probably preyed only on the caterpillars of *Cydia packardi*, and not on the maggots of *Rhag. basiola*.

Evidences to this end are twofold. First, the rose hip fly was not reared from hips taken at San Jose, and was infrequent at Mahomet and Velma. Second, the habits of the cherry fruitworm favor the entrance of the predators into its burrow or mine, while those of the hip fly do not. The larvae of *packardi* perforate the hypanthium when they enter from the eggs, and subsequently prepare one to four holes to the outside where they eject pellets of excreta. Especially the latter type of holes made by the larger instars are likely to afford entrance for the slender clerid larvae. This may explain why the victims are usually large. The further fact that much of the excrement is ejected to the outside, or, when left in the mine, takes the form of semihard yet penetrable pellets, indicates the predators may pervade the mines to locate the caterpillars, and to attack them at the defenseless caudal end. By contrast, the larvae of *Rhag. basiola* enter the hypanthium through the inner end of the egg pit, which becomes plugged externally with dried hip substance, make no holes through the skin of the hip until they are full-grown and ready to emerge, and more or less fill the mine behind them with wet pasty obstructive excrement. Thus, the maggot inhabits a space that appears effectively sealed off against access of the clerid predators, whereas the caterpillar of *Cydia packardi* inadvertently provides an entrance and thereby makes itself vulnerable to predatory attack.

Carposina scirhosella H. S., CARPOSONIDAE, LEPIDOPTERA

In a footnote to an article that describes a new *Megastigmus* from *Pseudotsuga*, Wachtl (1893) gives the names of several species of insects that inhabit the hips of roses. Among these is a "Gelechiid moth, (*Carposina scirhosella* Tr.)." He gives no references to literature, and my search of the Zoological Record, 1893-1951, and series A of the *Review of Applied Entomology*, yielded none. The genus and species were named by Herrick-Schäffer in 1855 (Horn and Schencking, 1928). It is recorded from southeastern Europe and Asia Minor (Meyrick, 1913).

An idea of its probable habits may be gained from published studies of its generic relatives. In New Zealand, the larva of the raspberry-bud moth, *C. adreptella* Walk., bores into leaf buds, fruits or the succulent shoots, and may feed on leaves, or migrate from bud to bud to obtain sufficient food (Jeffreys, 1939). The larvae of *C. sasakii* Mats. bore into the fruits of apple, pear and others, where they complete their growth. Pupation is in the soil. It has been observed in Japan and Korea (Muramatsu, 1927).

THE SCAVENGEROUS FLY, *Lonchaea polita* SAY, LONCHAEIDAE, DIPTERA

This is a sturdy bluish black fly about 3.5 mm. long, with long wings that extend far beyond the end of the abdomen. The larva is believed to feed on the excrement and/or plant refuse caused by the feeding of the larvae of *Rhagoletis basiola* and *Cydia packardi* in the hypanthium of rose hips, and in similar hosts. Some puparia were found in the abandoned mines of these phytophags, and adults emerged from old hips kept in fruit jars. Although not numerous, this is the principal scavengerous animal known to me from hips.

I obtained a series of 36 individuals from jars of rose hips, and one from nature. The hips originated in Minnesota, Wisconsin, and Illinois. All the 36 flies were reared at Urbana, Illinois. Four of these are now in the collection of the United States National Museum. The rest bear data as follows:

Eaglesnest, Minnesota, three from *Rosa blanda*, July 31 and August 9, 1946.

Gordon, Wisconsin, 10 from *R. blanda glandulosa*, June 11 to 20, 1946.

Urbana, Illinois, one from *R. palustris*, June 17, 1947; one from *R. virginiana*, July 12, 1947.

Pana, Illinois, two from *R. carolina*, June 11 to 12, 1946.

Philo, Illinois, 16 from *R. carolina*, June 9 to 14, 1946. Also four empty puparia found in old hips in jars, June 14, 1946. This shows that the larvae pupariate in the hip, and do not emerge to transform on the ground, as *Rhagoletis* does.

Pechuman (1937) reared numbers of *L. polita* from elm logs, usually in association with bark beetles, and stated it is probably a facultative parasite of scolytids, although usually acting as a scavenger. On the other hand, Kaston (1939) believed it to be predatory on the elm bark beetle, *Hylurgopinus rufipes* (Eich.), in whose egg galleries the fly pupates. Claassen (1921) gives an account of this fly in his report on insects associated with *Typha*. Dr. C. W. Sabrosky, who identified my specimens, commented in his report to me that *polita* is "undoubtedly a scavenger, following damage by other insects."

THE ROSE CURCULIO, *Rhynchites bicolor* (FABR.), CURCULIONIDAE, COLEOPTERA

Common names. This red-and-black beetle, sitting on rose buds and boring into their sides with its long proboscis, is a familiar and unwelcome insect (Fig. 33). It is the best known of the several species of

insects that develop in rose hips. Popularly it goes by the name "rose bug," and in the literature is referred to variously as the "rose snout beetle," "red rose beetle," "rose weevil," "black-snouted rose beetle," and "rose bud curculio." However, "rose curculio" is the official common name adopted by American entomologists.

Taxonomy. Fabricius (1792-94) described this North American species under the generic names *Attelabus* and *Curculio*. Herbst (1796) established the genus *Rhynchites* and assigned *bicolor* to it. Sharp (1889) subdivided *Rhynchites* into further genera, one of which was *Merhynchites*, which included *bicolor*. Pierce (1913) adopted Sharp's new genera and his placement of *bicolor* in it. Thus the name of this beetle became *Merhynchites bicolor* (Fabr.). Moreover, Pierce (1913) recognized six varieties of *bicolor* in North America, four of them new to him, which were based largely on differences in color. Following are the six varieties, with their then known geographical distributions as cited by Pierce.

M. bicolor bicolor (Fabr.): Washington, D.C., New Hampshire, Maine, Massachusetts, Manitoba, New Jersey, Wisconsin, Iowa, Utah, New Mexico.

M. b. wickhami Cockerell (Cockerell, 1912): Vancouver, British Columbia; Washington, Oregon, California, Idaho, Utah, Wyoming, Montana, Colorado, Arizona, New Mexico, North Dakota.

M. b. cockerelli Pierce: California, Idaho, Utah, North Dakota.

M. b. ventralis Pierce: South Dakota.

M. b. piceus Pierce: Oregon.

M. b. viridilustrana Pierce: Arizona.

Buchanan (1939) reexamined the genera of Sharp, and, for reasons given by him, suggested that *Rhynchites* be temporarily retained in its broad sense and that the name *Rhynchites bicolor* (Fabr.) be continued for the rose curculio.

As regards the varieties recognized by Pierce, Green (1920) believed that some of the forms are capable of specific definition by means of constant structural and sculptural differences. I am inclined to agree with this view for the reason that *Rhyn. b. bicolor* differs definitely in some of its bionomic features from *Rhyn. b. wickhami*, which Hoerner (1936) investigated in Colorado.

Distribution. Chittenden (1901) enumerated the records from specimens in the collection of the U.S. National Museum, and Pierce later (1913) did the same. Since these reports are generally available today, I do not repeat their data here, but give only the records known to me from later publications, and those added through my own studies.

Massachusetts: Woods Hole (Cockerell, 1912), Worcester (Gates, 1909).

Connecticut: New Haven (Britton, 1928).
New York: (Crosby and Leonard, 1922; Griswold, 1937); New York City (Blatchley and Leng, 1916).
New Jersey: (Smith, J. B., 1899); New Brunswick (Dickerson, 1910).
Ohio: Oak Harbor, West Lafayette, Homeworth (Balduf, original).
Michigan: Flint (Pettit, 1927).
Indiana: Idaville, Jamestown (Balduf, original).
Illinois: Many localities in northeastern quarter of state (Balduf, original).
Wisconsin: From Solon Springs south to Madison, along U.S. highways 53 and 12 (Balduf, original).
Minnesota: (Lugger, 1899); St. Paul (Marcovitch, 1916).
Oklahoma: Norman (Balduf, original).
Kansas: Manhattan (Balduf, original).
Nebraska: Crete (Balduf, original).
North Dakota: Crosby (Truax, 1946).
Manitoba: (Robertson, 1923).
Saskatchewan: (Twinn, 1933); Saskatoon (Balduf, original).
Alberta: (Twinn, 1933).
British Columbia: (Ruhmann, 1933).
Montana: "Far into the mountains" (Cooley, 1925).
Idaho: Moscow (Balduf, original).
Oregon: (Zeller and Schuh, 1944); Russellville (Lovett, 1915).
Colorado: (Cassidy, 1888; Cockerell, 1912); many localities around Fort Collins, up to 10,185 feet altitude at Leadville (Hoerner, 1936).
Utah: Mapleton in Utah Co.; Mt. Timpanagos, 6,800 feet, near Provo (Balduf, original).
California: Towle, Placer Co. (Branigan, 1915).
New Mexico: (Cockerell, 1894, 1912, Riley and Howard, 1891); Santa Fe (Cockerell, 1894).

I have not taken *Rhyn. bicolor* itself in northeastern Minnesota, but two of its hymenopterous parasites obtained here indicate it occurs in small numbers. The parasites are *Zatropis rosaeccolis* and *Luchatema baldufi*, reared from rose hips from the Cascade river near Lake Superior and from Ely, respectively.

LeConte and Horn (1876) reported this curculio as "an abundant species from the Atlantic to the Pacific coast." Blatchley and Leng (1916) added that it "ranges from the Atlantic to the Pacific, but principally northward in the Transition Life Zone." The thirty-fifth line of latitude marks the approximate southern limit of its occurrence, whence it seems to extend northward somewhat beyond the fiftieth line in the Canadian provinces. Were all the records from insect collections assembled here, they would probably show that *R. bicolor* occurs in all the states and

provinces within these limits. These coincide approximately with the known boundaries of the rose hip fly, the cherry fruitworm and the native rose seed chalcid.

Host plants of Rhynchites bicolor bicolor. As defined here, a "host" is the plant from which the larva derives its food and shelter while developing through its several instars. As applied to the eastern or typical form of the rose curculio, "host" excludes plants on which only the adult may be found to feed. Accordingly, only species of the genus *Rosa* constitute the host plants of this variety as observed to date in the eastern states.

I have obtained what are probably the larvae of *Rhyn. bicolor bicolor* from the hips of rose species as follows: *Rosa blanda*, from Solon Springs to Endeavor, Wisconsin; *R. arkansana*, Madison, Wisconsin; *R. a. suffulta*, Huntley, Illinois; *R. suffulta*, Manhattan, Kansas; *R. carolina*, Chetek to Endeavor, Wisconsin; *R. carolina*, many localities in the northeastern quarter of Illinois, and Idaville, Indiana; *R. palustris*, Homeworth, Ohio and Urbana, Illinois; *R. virginiana*, Fox Ridge State Park, Charleston, Illinois; *R. Macounii*, Crete, Nebraska; *R. rugosa*, Urbana, Illinois. Larvae presumed to be this species inhabited hips of a *Rosa* species that were sent to me from Norman, Oklahoma.

The following host or food records for *Rhyn. b. bicolor* are taken from the literature: *Rosa rugosa*, New Brunswick, New Jersey (Dickerson, 1910); Worcester, Massachusetts (Gates, 1909); St. Paul, Minnesota (Marcovitch, 1916); and New York (Blatchley and Leng, 1916; and Griswold, 1937). Also Lugger (1899) reported roses as the host of this curculio in Minnesota.

Food plants and injury. Information available to date indicates that the adult of *Rhyn. b. bicolor* feeds only on plants of the genus *Rosa*. A single dissenting record is the statement by Griswold (1937) that the beetle also gnaws holes in flower buds of peonies (*Peonia*).

When attacking *Rosa*, the curculios may utilize floral parts, hips and also vegetative parts of the plant. However, they appear to prefer the new, unopened flower buds. These form a conical structure of convenient size and shape to be embraced by the legs, and the tender corolla is readily penetrated by the long curved proboscis. Sometimes the snout pierces an overlying sepal as well. The filaments and anthers of the stamens within the lumina of the buds are thus accessible to the beak, and constitute no little part of the beetle's food. While the injury done to flower buds is less conspicuous than that to the flower, it is actually more serious and deep-seated, for buds may open imperfectly, or they may fail to open, remaining in place to die and dry up intact.

The injury done to the petals is most conspicuous and may come about

in one of two ways. First, and chiefly, a straight row or series of several holes of uniform size and shape appears on a petal, or on several adjacent petals. These originate when the proboscis bores through several petals or layers of the intact bud, and become apparent when the bud opens into a flower. Secondly, the holes thus formed may be enlarged after the petals open. But such enlargements seem to occur infrequently on *Rosa carolina* for the reason that the waxy surfaces of open petals afford but insecure footing to the beetle desiring to feed, and also the mandibles cannot readily seize the smooth surface and remove bits to ingest. But when the beetle stands on the comparatively rough-surfaced overhanging sepal or leaf, or on the pistillary center of the flower, its footing is secure, and from such a position of advantage, it has been seen to reach over to adjacent punctured petals and feed. The hole is enlarged by gnawing away the margin. Also it may then bore into, or clip the edges of, previously uninjured petals, or penetrate into the incipient hip under the pistils. Thus the open flowers may, in extreme cases, be reduced to tatters.

The tender, newly developed terminal shoots of branches, the leaf buds and succulent new leaflets appear to be secondary choices when flowers and buds are available at the same time. I have observed three circumstances in which vegetative parts are eaten, first when some beetles emerge from the ground before the flower buds develop; second where these buds will not occur as a result of severe pruning of the plants late in the spring; and third, when the crop of floral buds and flowers is inadequate for large populations of curculios.

The injuries to hips of *Rosa carolina* observed on the university campus at Urbana may be regarded as of two kinds. First are the pits or tunnels bored directly through the hypanthium by the female for deposition of her eggs. These are usually distinguishable by the covering of black secretion over the external opening. Second, and similar to the first, are the pits made by adults of either sex incident to feeding only; these contain no eggs, and lack the external covering of black material. The feeding punctures almost invariably occur on the petiolar or basal half of the hip. This area is utilized for the same reasons that it is employed for oviposition by *Rhag. basiola*, as stated above. Not only the hypanthium but also the achenes may be ingested insofar as the proboscis is long enough to penetrate to the inner cavity of the hip.

The extent of the damage inflicted on cultivated roses by *Rhyn. b. bicolor* is shown by the following instances. According to Gates (1909), the beetles ruined practically every bloom of *Rosa rugosa* at Worcester, Massachusetts, and their feeding extended even to clusters of tender, unfolding leaves. Dickerson (1910) reported that the beetles fed first in floral buds and flowers of *R. rugosa* at New Brunswick, New Jersey,

then attacked the hips so extensively that almost all bore one or more punctures. Also pertinent here are two of the more serious instances of injury to cultivated *R. carolina* at Urbana, Illinois. On June 22, 1949, a random sample of 573 hips checked in the field showed 40 per cent had been punctured by feeding or ovipositing adults. Since the period of adult life had not terminated on that date, the level of injury for the season eventually became higher. At another station, in a sample of 426 hips examined July 4, 1949, the over-all injury reached 37 per cent.

At Urbana, I found that the extent of damage varied not only from year to year but rose species to rose species and also from one part of a garden or hedge to another. Several explanations are suggested by these observations, as follows: unequal parasitism of the larvae in the several rose plantings; cultivation of the soil while the diapausing larvae and pupae inhabited it; the texture or penetrability of the soil to the emerging young adults and the descending mature larvae; isolation of plantings by intervening obstruction such as large buildings, trees and shrubbery; immunity of some rose species to attack, and the tendency of the beetle to concentrate on parts of a planting where an abundance of blooms occurs.

For example, *R. carolina* bears few flowers in dense shade. On July 4, only two per cent of the hips in the shaded part of a hedge bore punctures, while two parts growing in sunlight had been punctured to the extent of 47 and 50 per cent, respectively, on that date. By contrast, a fine long hedge of *Rosa hugonis* which consistently bore heavy crops of sizable hips year after year completely escaped attack by all phytophagous associated with rose hips, probably because it flowered before the reproductive adults emerged at neighboring plantings of other rose species.

The bionomic features of *Rhyn. bicolor* as recorded by observers in the western mountains and in the eastern area of the United States are so divergent that separate treatments of western and eastern forms seem most expedient. The known facts for the eastern form, which, according to Pierce (1913), appears to be the typical subspecies, *Rhyn. b. bicolor* (Fabr.), will be given first, followed by an account of the subspecies known in the west. Several of the forms delineated by Pierce occur in western North America. However, of these, only *Rhyn. bicolor wickhami* Cockerell has been identified subspecifically by the investigators. We are indebted to Hoerner (1936) for his recent comprehensive study of this form in Colorado.

Rhynchites bicolor bicolor (Fabr.) in the East

Adult (Fig. 33). According to Pierce (1913, p. 371), "the typical

specimens have elytra, prothorax, and base of head to the eyes red, the remainder of the body black. These specimens usually have the elytral strial punctures quite plainly larger than the interstitial punctures. The front between the eyes is moderately punctate, and rugose near base of beak."

Emergence. In my personal observations at Urbana the young pale reddish adults, after shedding their pupal cuticles, came up out of their pupal cells in the soil of the rearing pots in May to June, digging out from depths varying from one to four, but mostly two to three, inches. The length of time required for emergence was not determined, but is certainly affected by the physical properties of the soil. In 1947 the peak of emergence per day was reached in approximately 20 days after the beginning of issue; in 1949, this figure was 16 days.

Locomotion. Besides its six legs for crawling over the plant, the beetle flies readily from bush to bush, particularly when the local supply of rose buds is diminishing, and, as many entomologists have observed, it promptly folds its legs under itself to fall, usually to the ground, when disturbed by the abrupt approach of people. It is presumed that the plant is reached again by crawling. These activities, and especially flight, are performed more freely at higher atmospheric temperatures. The red color or odor of the *carolina* rose appears to stimulate a positive response in the flying beetle: an individual, during a flight of three feet, passed over a red rose about two feet below, and made an abrupt U-turn back to the flower, landing precisely upon it. When the waxy petal provided no foothold, the beetle clung to an adjacent leaf, from which it could reach the flower with the proboscis. Proximity would have indicated feeding on the leaf, but, due to some sensory reaction, the petal was preferred. Additional performances of similar kind were observed.

Copulation. This activity seems to begin when the beetles have been out of the ground about 10 to 15 days. Since emergence at Urbana begins about mid-May, copulation commences near June, and, where larger numbers of beetles were concentrated locally, continued past the middle of July. The male climbs to the dorsum of the female, where the union is effected. During the period, the somewhat larger female may crawl about and engage in feeding. Not infrequently one may see a male approach another adult, but instead of entering into the mating position, turns aside at once. Such behavior probably means that the individual approached is another male, or, that males cannot identify the sex of their species until they make physical contact.

The proboscis sometimes comes into use in the activity of mating. On one occasion an aggressor, presumably a male, assaulted a mating pair by inserting his snout between the two, and after some failures, succeeded in separating them.

Oviposition. Dickerson (1910) noted that *Rhyn. bicolor* rarely fed on the tender tips of *Rosa rugosa* branches at New Brunswick, New Jersey, and he made careful search of the punctures to determine if eggs were laid in the branches. He found no eggs in them. When pursuing the larval life of *Cydia packardi*, at Urbana I examined hundreds of the flower buds of *Rosa carolina* which also bore punctures made by the rose curculio. In no case did I find eggs of the beetle in these buds, and, moreover, I did not discover the beetle engaged in oviposition in buds.

Samples of hips which bore beetle punctures, picked at intervals of three days to two weeks through June to August of 1947 to 1951 were also dissected. I found good numbers of eggs, and larvae of various sizes, in the bottoms of the egg pits in the hypanthium or in the achene cavities of the hips.

As a further check, I again inspected quantities of *R. carolina* buds at Urbana from May 21 to June 4, 1955, when both flower buds and the rose curculio occurred. A good percentage of the buds bore punctures made by the proboscis of the beetle, but none such contained eggs. At the same time, a high proportion of new hips were found to contain eggs and first instars, showing that oviposition was in progress when the buds were being inspected.

From these positive and negative results, I conclude that the eggs of *Rhyn. b. bicolor* in Illinois, and probably also in states to the east, are laid only in the hips. However, further explorations in the northern midwestern states are desirable in view of the observations by Marco-vitch (1916) in Minnesota. He reported differences in susceptibility of rose varieties to oviposition by *Rhyn. bicolor*, having "found that in the form, *Rosa rugosa*, the common Japanese rose, the eggs are laid within the hips, and not in the flowers or elsewhere. However, with *Rosa rugosa alba*, a white variety, the larvae were found within the flowers on July 22, to be already about half-grown. It appears, then, that in this variety, the eggs are laid in the flowers, and later [the larvae] may crawl into the hips."

Oviposition in the hip of *R. rugosa* is described by Dickerson (1910). When excavating the egg pit with her beak, the beetle spreads her legs as if to brace herself. The boring continues until the beak is inserted to the eyes, and the antennae are pressed close together and upward against the top of the head. The final operation "appeared to be the smoothing down of the sides of the puncture and enlarging the bottom; the whole operation taking somewhat over a quarter of an hour. . . . Having completed the puncture, the insect turned about, rested its anal extremity in the cavity, and remained there for about half a minute while it oviposited. Then turning about again, it spent slightly more than half a minute in apparently pushing the egg down into the bottom of the

cavity and covering the opening. . . . Whether the covering of the puncture is a secretion of the plant caused by the injury, or in part is some secretion of the weevil is not quite evident. At any rate, it forms a distinctive covering, light in color at first and gradually darkening." Several times I watched the beetle oviposit, and found the procedure is essentially as described by Dickerson.

Marcovitch had reported previously (1916) that the "egg-laying puncture" can be distinguished from the feeding punctures in being blackish and covered over, with no noticeable depression. I have repeatedly confirmed that such a black covering is constructed over the mouth of the egg pit, and that it is lacking where eggs have not been inserted. I have only circumstantial evidence to support my belief that the black covering substance originates in the beetle, not from the hip. First, when the cover is being formed, the beetle stands with the end of the proboscis introduced into the mouth of the puncture, then manipulates the mouth parts rapidly and produces a heavy gray-brownish fluid. This may be regurgitated food, a salivary secretion or both. Were it plant sap oozing from the wound, a black covering would form also over feeding punctures. Not infrequently, solidified plant sap or protoplasm from the punctures plugs the pit below the outer surface. Such plugs do not turn black. Further, when one carefully dissects off a piece of the black cover from egg pits, he finds it is uniformly thin and slightly transparent. These characteristics suggest it was laid down and molded by a mechanism capable of controlled manipulation, such as mouth parts, and not a product poured out by chance from a wound in the hip. The cover lies over the center of the somewhat star-shaped scar within which the pit is located. The scar is formed as the mandibles scoop out bits of hypanthial skin preparatory to boring of the egg pit.

The shiny, coal black covers not only are almost certain indicators of oviposition, but also of the extent of embryonic development. With enlargement of the hips, the covers become split into pieces whose number and extent of separation roughly indicate the time elapsed since oviposition and thus also the approximate age of the embryos. However, if the hip is already full-grown when the egg is laid, the cover remains intact and has no such indicative value.

The deposition site of the eggs of *Rhyn. b. bicolor* varies within the hips of *Rosa carolina* investigated for the most part at Urbana. Some occur within the hypanthium when it is of such thickness that the snout cannot reach the achene cavity. However, most eggs are found in that cavity. They are set in a hole gouged in a single achene, or in a receptacle chewed out between two contiguous achenes, or lie free upon the peripheral fruits. Rarely, an egg lies amid the pollen tubes in the apical half of the achene cavity; in such instances it may have been inserted through

the natural aperture at the floral end of the hip. Almost without exception, the deposition sites occur within the basal petiolar area of the hip. Variations in the size, "set," age, or species of the hip determine the depth to which the beetle can penetrate. In the course of the fruiting season, *R. carolina* produces several "sets" or clusters, whose component hips generally are successively smaller as the season advances. When most ovipositions coincide with maturing of the first cluster, a larger number of eggs should logically be found within the relatively thicker hypanthium than when oviposition coincides chiefly with the maturing of the smaller later hips whose hypanthium is relatively thinner and thus more penetrable by the proboscis.

Egg (Figs. 34, 35). The egg is subrotund, its ends very broadly rounded, with one end perceptibly wider than the other. In size, it averages 0.95 mm. in length, 0.8 mm. in height at the middle, and 0.75 mm. in maximum diameter. Some eggs found in the hips are covered with a thin layer of whitish frostlike material, which presumably originates in the reproductive tract, and peels off readily when the egg is removed from its nidus. The bared egg, when still young, appears shiny, smooth, hyaline and pearly whitish, later becoming yellowish as the embryo within approaches maturity. The chorion is tough and leathery, and the egg so turgid and resilient as to be held with difficulty with needles, and sometimes pops audibly when punctured.

The advanced embryo takes on the form of the larva which then becomes visible through the chorion, and the reddish mandibles may be seen to open and close as when chewing food. It therefore seems certain that these mouth parts later serve to rupture the chorion in the process of hatching.

Larva (Fig. 36). The larva of *Rhynchites bicolor bicolor* is the only phytophagous form of insect that lives free in the achene cavity of the rose hip. Structurally the larva is legless and white, excepting the exposed part of the head and mandibles, which are brown; the body is moderately curved, the anterior end thicker. The head is almost entirely retracted into the thorax. The postcephalic segments have prominent transverse folds that bear a few short bristles. The number of instars comprising the larval stage has not been determined but, whatever it proves to be, all have the general features stated above. In their normally curved posture, these robust grubs range from about 1.0 mm. to 3.0 to 5.0 mm. in length in the course of growth from hatching to maturity. The variation in size of the full-grown larvae emerging from the hips is to some extent associated with latitude, or, more specifically, perhaps with differences in climate. For example, both the larvae and adults reared from *Rosa carolina* and *blanda* taken at Chetek, Wisconsin, are

visibly smaller than those from *R. carolina* grown at Urbana, Illinois. The cuticle of the larvae is pearly white, but the body of the first instars appears reddish after they have fed on achenes. As they approach maturity, the larvae accumulate an increasingly larger amount of whitish adipose that lends the body a dull chalky appearance.

Small numbers of larvae were discovered within the egg pit in the hypanthium, from which location some migrated to the achene cavity. The larvae from eggs deposited in an achene commonly made the achene their nidi and fed on the contained seeds. These afforded food enough for the first instar, for the exuviae were sometimes found in the achenes. Sometimes also second instars occupied the achenes in the same manner, at least for a part of the stadium. Not infrequently, the aperture chewed in the occupied achene by the ovipositing female was so obscured with frass that the larvae were not readily discovered. The fact that these small larvae leave the shells of the achenes intact, except to enlarge the exit holes, is evidence that they ingest chiefly the nutrient dicotyledons within. Also when eggs are laid in the concavity shared by two adjacent achenes, the small larvae eat the seeds. Small larvae sometimes feed for a short time on the inner face of the hypanthium. These individuals seem to originate from embryos located in the inner extremity of the egg pit.

From these several initial egg sites, the growing larvae gradually eat their way deeper into the cavity, creating ever increasing amounts of a sawdust-like pale brown frass. This certainly consists in part of hard, dry bits of ripe rose seeds and in part of excretal pellets, but largely of particles of achene shells broken up in the process of feeding. Consequently, the large larvae are often found deeply embedded in a mass of frass and whole achenes deep in the center of the basal half of the achene cavity. The achenes present in any one hip vary considerably in number; hence some hips may conceivably contain food matter inadequate to enable a larva to realize its growth potential. In such cases, the larva might complete its growth by feeding on the inner face of the hypanthium, thereby perhaps causing the dark discolored areas sometimes visible externally on the hip.

Mortality. Some fatalities occur among both the embryos and the larvae of the rose curculio. Occasional embryos may die from two possible causes: first, from being encased in the solidified protoplasm that has oozed from the ruptured tissues along the wall of the egg pit; second, the female beetle may break some of her eggs as she pushes them deeper into the pit with the hard, pointed proboscis. Some dark, dead embryos and collapsed chorions have been found that suggest these causes.

With the earlier instars, I have repeatedly suspected cannibalism where two or more black-covered punctures occurred in a hip but only

one larva was found, although I have obtained no good direct evidence to support this theory. However, ectoparasitism by chalcid larvae of *Eurytoma* spp. and *Zatropis rosaealis* unquestionably accounts for some failures to find curculio larvae where black covers indicated they should be present. More persistent searches occasionally disclosed the shrunken dead dark bodies of small *Rhynchites* obscured amid frass in the hip cavity along with full-grown larvae or pupae of the parasites or their remains. Although the endoparasitic larva of the ichneumonid, *Luchatema baldufi*, sometimes inhabits large percentages of the host larvae, including the smaller instars, it does not cause mortality while the host resides in the hip.

Emergence. The full-grown larva of *Rhynchites* works its way through the frass in the hip cavity to the inner face of the hypanthium, and makes a hole, usually through the basal half of the hypanthium, to escape. En route, the larva ingests at least some of the usually red hypanthial material, as indicated by reddish substance in the food canal of some newly emerged larvae. Emergence is sometimes heralded by the appearance of an external discolored patch above the spot in the hypanthium where the larva will issue.

How long the emerged larvae remain above ground in nature was not observed. However, numerous individuals removed from hip jars and placed on soil in flower pots were seen to lose no time in burrowing into it. The larger larvae that had been out of hips in jars as long as 24 hours remained vigorous enough to bore down promptly when soil was provided.

Influence of temperature. While removing emerged larvae from hip jars in the falls of 1945 to 1947, I gradually became aware of an unexpected relation between emergence and atmospheric temperatures. Instead of increase in warm days and decrease on cold days, it was found that a much greater number of larvae emerged from hips at lower than at higher temperatures. To check on this interrelation of emergence and temperature, I secured large quantities, usually one to several thousands per year, of hips from wild *Rosa blanda* and *R. carolina* at Chetek, Wisconsin, early in September of 1948 to 1951. Brought to Urbana, Illinois, the hips were stored each fall in jars kept under approximately natural temperatures, where the mature larvae emerged in September and October. Day-by-day records were kept on the numbers emerging during most of these yearly periods. The daily crop of larvae was removed from the jars at the close of the day. The temperatures recorded below pertain to an approximate 24-hour period preceding the daily removal of the emerged larvae. (See Table 2, p. 90.)

To illustrate this relationship of temperature and emergence, data

TABLE 2. RELATION OF TEMPERATURE TO EMERGENCE OF
LARVAL *Rhynchites bicolor bicolor*
(September 14 to October 6, 1948 and 1950)

Extremes of temperature		Number of larvae emerged	Per cent of 2,626 larvae issued at various temperatures
Low	High		
34-40° F.	55-69° F.	676	25.75
41-47°	61-75°	809	30.81
48-54°	64-83°	829	31.57
55-61°	64-90°	233	8.87
62-69°	74-94°	79	3.00
		2,626	100 per cent

(Table 2) were chosen for the period, September 14 to October 6, for both the years 1948 and 1950, when daily records were taken consistently. Kept in temperatures approaching those of natural conditions (an open shelter enclosed with wire screens), the lots of hips yielded a total of 2,626 mature larvae. In the table, the emergence records are grouped into five categories graduated chiefly in accordance with the range of the low extreme temperatures. It will be readily understood why these low ranges are not quantitatively equivalent to the spread shown by the high extremes, since day and night as well as daily temperatures in nature are subject to inconstant or differential variation.

Briefly interpreted, the percentile data in Table 2 indicate that the large majority, or 88 per cent of the 2,626 larvae, emerged from the hips at relatively low temperatures of 34 to 54° F., and only 12 per cent at the higher levels of 55 to 69° F. It appears also that temperatures around freezing, or 34 to 40°, are not quite so effective as activators as 41 to 54°, yet are greatly more so than temperatures of 55 to 69° F.

The daily records, involving 44 days in the 2 years, demonstrate the pattern of alternation or fluctuation between peaks and troughs in the phenomenon of emergence more patently than the data of Table 2. From these it seems evident that the major activity of the larvae in the hips is of two comparatively distinct types. One, they engage in their prime function of feeding-growing at the higher temperatures, and as a consequence, a fraction of them becomes full-fed, mature, and conditioned for emergence. The number of emergence-ready larvae accumulated during this phase depends on the duration of the higher temperatures that favor development. Two, the matured larvae so accumulated in the hips engage in the alternate activity of emergence when the atmosphere of night, or fall days, cools decidedly. However, there is rarely observ-

able a complete line of demarcation between the above two types of activity, i.e., neither the feeding-growing nor the emergence function is completely inhibited, except possibly in late fall. Very few, if any, larvae fail to attain the emergence-ready condition on account of prohibitory low temperatures.

Two instances are cited here from the daily records that reflect the alternating character of the larval activity in an impressive way. First, on the four days, September 18 to 21, 1948, when the 24-hour periodic temperatures ranged high, from 60 to 94°, only three larvae emerged: in the next four days of comparatively cool weather, September 22 to 25, temperatures varied between 44 and 77 degrees, and 335 larvae issued from the same hips. Second, in the three days, September 20 to 22, 1950, at extreme temperatures of 58 to 85°, 143 larvae issued: September 23 to 25, when temperatures fell to 37-72°, 766 larvae emerged from the same hips.

It may then be deduced that a species that exhibits two such opposite characteristics can have evolved, and is able to perform successfully, only under climatic conditions characterized by alternation of periods of lower and higher temperatures. Accordingly the basic reason for this association of two antipodal behavioristic characteristics lies in the fact that the immature larvae and the mature larvae are physiologically two distinct entities despite their conspecificity. The first is geared to feed and grow in higher temperatures, and is congenial to a limited dark space within a hip, a situation favorable to growth. The mature larva no longer feeds, and seeks the large open spaces by emerging, to adopt an entirely different mode of life thereafter. In fact, this "mature larva" is to be regarded as a prepupa, with physiological characteristics distinct from those of the immature larva.

Weights of mature larvae. More than 2,000 mature larvae available in the fall of 1950 and 1951 were utilized in a study of their weight characteristics. One thousand eight hundred twelve larvae emerged from about 1,800 hips gathered from *Rosa blanda* and *R. carolina* at Chetek, Wisconsin, on September 5, 1950, and 392 were reared from 2,262 hips obtained from the same sources on September 6, 1951. The daily yields were weighed collectively within one to 24 hours after the larvae emerged.

The total mass of 1,812 larvae reared in 1950 amounted to 26.307 grams, and the average weight per individual larva was 0.0145 gram. The corresponding data for the 392 larvae of 1951 were 5.528 grams and 0.0141 gram. Thus, the average weights of individuals for the two years were very nearly identical. Of greater interest, however, is the steady, progressive reduction in these average weights during the 49-day season of 1950, September 8 to October 26. The average individual weight of larvae

that emerged in the first week was 0.0159; in the final week, it had decreased to 0.0119 gram. The weighed larvae of 1951 issued in eleven weeks. The average larva that emerged in the first week weighed 0.0156, whereas that of the tenth week weighed 0.0118 gram. In this year, the weekly decline was less regular than in 1950, and the weekly samples consisted of only 5 to 95 individuals, as compared with 15 to 901 in 1950. How may this seasonal reduction in weight of individuals be accounted for?

The larvae feed almost entirely on seeds. These are ripe by September 1, and remain in good preservation in storage. Thus, the condition of their food is probably not an important factor in the over-all reduction in the average weight of the larvae. Instead, it is likely that the progressive lowering of average temperatures as the fall season advances, favors less and less of feeding with resulting smaller larval bodies, while at the same time, this cooler average weather stimulates the emergence of the larvae. Their smaller size and lower weights indicate that many may emerge before they attain the maximum of which they are capable under warmer conditions.

Gas in the digestive tract. My notes contain references to 23 instances in which varying amounts of a clear gas were discovered in the larvae of the rose curculio. Still other cases were not recorded. Where the gas was specifically located, it occurred in the crop, which is a large bulbous sac in this species. When the inflated crop was punctured, a series of small bubbles escaped into the water in the dissecting dish. Larvae of all ages, from first instars that had taken some food, to mature individuals recently issued from the hips, contained gas. In all cases, the larvae affected contained some food stuff in the crop.

Larval life in the ground. If one may make a deduction from their leglessness and their ineptness in locomotion on smooth surfaces, the larvae in natural environment probably fall rather than crawl to earth. Many of my newly emerged larvae were placed on black Illinois soil in four-inch flower pots. Here they began promptly to bore in, head first. Upon examining the "cages" weeks to months later, the larvae were found to have burrowed to depths of one to four inches, the large majority halting at depths of one and a half to two inches. In nature, the depth of penetration is obviously determined by the hardness of the soil, which may be so firm that exploratory crawling is required to find a penetrable place; or descent into the soil may actually be impossible.

Larvae that were later removed from soil in the pots had constructed oval cells that had a smooth inner surface, but not a well-defined periphery. The cells were formed of particles of soil cemented together with a substance that doubtlessly issues from the mouth, and is probably

glandular in origin. It permeates the surrounding earth to a thickness of several millimeters, being more compactly fused on the inner face and more loosely adherent toward the periphery of the cell, so that the external layer remains rough and crumbly. The over-all cell wall is about 3 mm. thick.

Under the somewhat artificial conditions of the soil pot, overstocked sometimes with 100 to 200 larvae, the cells lie so close together that the soil which surrounds them may become fused into a dense, firm, impervious, imporous gummy mass. Such a condition of the soil seems to induce a state of oxygen deficiency in the larvae, for when first removed, although appearing normal in color and form, they have been observed to remain inactive, as if dead, but resume activity on exposure to the atmosphere for an hour or so.

Larval diapause. Concealed within their cells, the larvae lie in the ground for eight to nine months, from about September to May. This was established by unearthing larvae from soil pots during November to June. In that time, they undergo no change in external appearance or internal condition so far as gross physical observations can disclose, and appear to lose little weight, as indicated by weighing a small sample unearthed after four weeks. The digestive tract is empty and collapsed from the beginning, excepting sometimes a small amount of red hyphal matter ingested as the larvae chew their way out of the rose hip. The body cavity is full of a grayish white soft adipose substance. In its disintegrated form in the pupa, it constitutes numerous small spherical particles. In submature and younger larvae, these are united to form large slab-shaped bodies, all of which are bound together to constitute one mass. All the other viscera are obscured or enveloped by this body, only the digestive tract retaining bulk sufficient to be readily identified.

This inert condition, or diapause, is exhibited by all mature larvae emerging from mid-August to November. Hence, the diapause is of a physiological type initiated during the larval life in the hip. This is the prevailing form of suspended development in the life of *Rhyn. bicolor*.

Prolonged diapause. The prolonged type of diapause first came to my notice when I scrutinized the soil in certain pots on July 14, 1947, and discovered nine mature larvae of *Rhyn. b. bicolor* still present a full month after emergence of adult curculios is usually completed. Dissection of the nine showed that seven individuals contained the parasitic larvae of the ichneumonid, *Luchatema baldufi*, which apparently inhibited the pupation of the hosts. However, the other two lacked parasites and remained normal in color, form and size.

The nine larvae emerged September 14 and October 27, 1956 from a quantity of hips gathered at Chetek, Wisconsin, that same fall. They had

wintered out of doors in soil pots, and were returned to the open-air shelter in early May for observation on development.

The two retarded, parasite-free mature larvae raised the question whether such individuals die sooner or later, pupate and become adult out of season, or may persist through a second winter and transform to adult in the usual spring season but one year late.

In the hope of obtaining the answer to these questions, I employed the larvae from another lot of hips picked at Chetek in September of 1948. The larvae were placed in ten soil pots, and set out-of-doors for the winter. Adult *Rhyn. b. bicolor* developed in these pots, and duly emerged in June of 1949. Inspection of the soil in two of the pots in the fall of 1949 revealed a few healthy larvae, several months after transformation was normally completed. These tardy larvae were replaced in a soil pot and kept under observation along with the other eight undisturbed soil pots of that set. The nine pots were set out into natural weather for the second winter, 1949-50, then returned to an open-air shelter for the following spring, when the soil was wetted thoroughly with water as needed. Fifteen normal adults emerged from the nine pots in the period of June 6 to 9, 1950, demonstrating that, under some conditions, the mature larvae do persist for an entire additional year and then change to pupae and adults in the usual period of transformation in June. Despite the prolongation of the larval life, the species conforms to the same seasonal distribution of the developmental stages as it does in the usual annual life cycle. Thus, the adult makes its appearance at the essential budding-fruiting time of the host plant.

Prepupa and pupa. Along in May, both the normal and prolonged diapauses of the overwintered larvae are terminated. The exertion of the head from its previously retracted position in the thorax is the first external indication that the prepupal body is formed within. The approach of the final larval molt is also betokened by the loosening and crumpling of the cuticle and the change of the body from the curled to a straight form. Internally the slabs of fat body disintegrate into a homogeneous mass of creamy white particles.

When the larval cuticle is shed after prepupation, all the external structures of the white pupal body are seen to have formed. The pupal cuticle bears a sparse set of bristles which appear to be arranged in constant positions (Figs. 37, 38). They occur as 3 pairs on the dorsum of the snout; 3 transverse rows on the pronotum, comprising a row of 13 on the anterior margin, a row of 4 on the disc, and a row of 13 on the hind margin; a total of 8 bristles on the disc of the mesonotum, arranged in two transverse rows of 4 each; bristles on the disc of the metanotum are the same as those on the mesonotum.

The dorsal abdominal segments have bristles on the rounded trans-

verse ridges as follows: first tergite, 12 bristles, with six on either side of the midline; second, 10, with groups of 2 and 3 on each side of meson; third, 10; fourth, 14, the median two small, lateral ones much larger; fifth, 12, in two series of 6 each; sixth, 10; seventh, one bristle on each caudolateral corner; eighth, 10, in an irregular transverse row; ninth, or terminal tergite, with an arcuate row anterior to the pair of strong, brown, caudal tapering spurs which are subparallel and directed dorso-caudad. There is also a pair of minute bristles on each of the humeral bulges of abdominal segments IV, V, and VI. The "knee" of each leg bears two apical bristles directed laterad. Ventrals of thorax and abdomen are bare.

Life cycle. Data from field and laboratory studies show conclusively that *Rhynchites b. bicolor* completes its life cycle once in about 12 months, excepting the minority of the population that may require two years due to a prolonged diapause in the mature larval state. Moreover, one cycle per year appears to characterize other varieties of the species wherever its development has been studied.

(1) Cycle at Urbana, Illinois. The statement below is based on data, and a few estimates, derived from several seasons of work with particular reference to the life of the curculio in *Rosa carolina*.

The diapausing mature larvae in their hibernacula in the ground begin pupation about May 5, and complete the transformation by June 18. Emergence of adults from the ground extends from May 20 to June 18; they continue abroad to August 7, the last date adults were seen. The over-all adult season is therefore about 80 days. The occurrence of newly laid eggs in hips shows that oviposition extends from June 10 to August 7, or about 59 days. Adding 10 days for embryogenesis gives an over-all embryonic or "egg" period of 69 days. The earliest first instars were found in hips on June 20, and the latest emergence-ready mature larvae occurred about October 15. Since the first larvae issued from hips on August 15, and such were still present in soil pots as late as June 8 of the next spring, the full-fed last instars have an over-all diapause plus wintering stage of approximately 298 days, or 10 months. When the 117 days of over-all life in the hip are added to the diapausing period, the rose curculio proves to be present, in one or another of its larval instars, a total of 415 days. Being more than a year, this means the earliest first instars may have hatched in June before the latest wintering larva has pupated in the same June. Pupae were shown to occur in soil pots between May 5 and June 18, or for 44 days. Estimating the pupal period as 15 days, adults may appear as early as May 20.

(2) Cycle at Chetek, Wisconsin. Although the life cycle of the rose curculio at Chetek probably differs from that described above for Urbana only in the initial and concluding dates of the several stages, a few

significant data should be given here. The 1,517 larvae obtained from hips of *Rosa blanda* and *carolina* early in September, 1950, at Chetek, were distributed chronologically in 13 soil pots, as they emerged at Urbana between September 13 and 25. At intervals during the period October 29, 1950, and July 19, 1951, the insect contents of sample pots were removed and identified to note their developmental status. The essential results follow.

Samples scrutinized in October and November contained only mature larvae in their hibernacula. In ever decreasing numbers, larvae persisted to July 13, 1951, some of these being parasitized by the ichneumonid, *Luchatema baldufi*, which destroys the mature larval host. Pupae occurred in the sample pots from May 4 to June 7, and adults were found only in the pots examined on June 7 and 15. The last five of the 13 cages, explored between June 21 and July 19, had yielded their adults, but contained numbers of the parasite, which varied from a few first instars in the host to many pupae in cocoons, and fewer adults not yet emerged from the soil.

(3) Cycle in Atlantic states. Additional data bearing on the life cycle of *Rhyn. b. bicolor* in the eastern United States are contained in the reports of Gates (1909) and Dickerson (1910). According to Gates, the adults were first noticed at Worcester, Massachusetts, late in May; they became more common in June and still remained numerous on July 10, when the observations were discontinued. At New Brunswick, New Jersey, Dickerson discovered that the adults appeared in May, and continued active through June and July. Oviposition persisted into late June, when feeding and copulation also were noticed. Hatching began there in the first part of July, and most eggs had hatched by mid-July, and no unhatched ones were found on July 22. Some larvae had matured by August, and many had become full-grown soon after mid-August. Very few immature individuals remained in early September, and most larvae had left the "seed capsules" at that time.

Marcovitch (1916) investigated an undetermined form of *Rhyn. bicolor* in Minnesota, probably in the vicinity of St. Paul. He first discovered the adults puncturing the buds of *Rosa rugosa* on June 10, and found eggs deposited within the hips on June 28. These hatched in 6 to 10 days. The larvae reached maturity about the middle of September, when they entered the soil and pupated the following spring.

Rhynchites bicolor in the West

Five of the six varieties of *Rhyn. bicolor* Fabr. recognized by Pierce (1913) appear to be more or less western in their distribution. These are *Rhyn. b. wickhami* Cockerell, *Rhyn. b. cockerelli* Pierce, *Rhyn. b. ventralis* Pierce, *Rhyn. b. piceus* Pierce, and *Rhyn. b. viridilistrana* Pierce.

The types of another variety, *Rhyn. b. erythrosoma*, described by Cockerell and Harris (1924), were taken at Boulder, Colorado. Excepting Hoerner (1936), who investigated the life of *Rhyn. b. wickhami* in Colorado, the writers have not specified the varieties with which they were concerned.

The bionomic differences in *Rhyn. bicolor* as reported by Cooley (1903) in Montana, Lovett (1915) in Oregon, Robertson (1923) in Manitoba, and by Hoerner (1936) in Colorado may prove to coincide with some of the varieties described by Pierce.

Following is an abridgment of Hoerner's (1936) description of the metamorphic stages of *Rhyn. b. wickhami*.

Adult. Thorax and elytra bright red; venter of body and femora, beak, tibiae, tarsi and antennae black. The original description (Cockerell, 1912) gives characteristics of sculpture, form and vestiture. Beaks of twelve males averaged 1.82 mm. in length; of fifteen females, 1.95 mm.

Egg. Pearly white, elliptical, finely pitted or reticulated; average size 1.24 x 1.1 mm.

Larva. Newly hatched, white, legless, robust, tough, about $\frac{1}{12}$ x $\frac{1}{25}$ inch when coiled; full-grown, about $\frac{1}{4}$ x $\frac{1}{8}$ inch, stramineous, subcylindrical, broadest through postcephalic segments three to five, tapering bluntly at ends; body strongly wrinkled; head retractile, its anterior third brown; pronotal shield pale, obscure; thoracic legs represented by enlarged setose tubercles; thoracic and abdominal segments sparsely and finely hairy; spiracles on all segments except 2, 3 and 12.

Pupa. White at first, about $\frac{1}{5}$ inch long by $\frac{1}{7}$ inch across mesothorax; a pair of curved appendages on caudal end of abdomen.

Hosts of western Rhyn. bicolor. Published reports of Cooley (1903), Lovett (1915), Robertson (1923), and Hoerner (1936) indicate that, in their areas, *Rosa* is the only plant group in which the larva of the rose curculio develops. Cooley (Montana) was never able to find larvae except in rose hips, and he concluded "this is doubtless the normal place for their development." While Lovett (Oregon) found eggs in the flower buds of blackberry, few hatched, and none of the larvae fed in the dead buds, indicating that blackberry is not a host plant. On the other hand, Lovett emphasized that the larvae feed in the "seed pods," i.e., hips of rose. In Manitoba, Robertson found the larvae feeding on seeds in the hips of some cultivated roses and in native species *Rosa acicularis*, *blanda*, *Macounii* and *suffulta (pratincola)*. The larvae of *Rhyn. bicolor wickhami*, the variety which Hoerner investigated in Colorado, develop in the mummified flower buds of roses.

In my own investigations, I have reared larvae of *Rhyn. bicolor* from hips sent to me from three places in the west. These presumably repre-

sent varieties other than the typical form, *Rhyn. b. bicolor*. The hosts and places were: *Rosa acicularis*, *lunelli*, *alcea*, *pyrifera* and *Macounii* from Saskatoon, Saskatchewan; *R. woodsii*, Mapleton, and Mt. Timpanagos, near Provo, Utah; and *R. ultramontana* and *spaldingi*, Moscow, Idaho.

Excepting the discovery of eggs in the flower buds of blackberry, by Lovett (1915), all the above records of host plants indicate that the larvae of western varieties of *Rhyn. bicolor* feed and develop in the hips, or in the mummied flower buds of roses. The exceptional case of blackberry may be questioned until it can be established whether or not the larvae can develop in the flower buds of this berry plant. In the light of these evidences, we are probably to interpret other reports of feeding on blackberries, raspberries and loganberries as having reference to the adult curculio, and, if so, these berry species are to be regarded as food plants, not as hosts.

Correction. Reference is made here to the short essay by Craw (1894) under the title "Attelabian Snout Beetle, *Rhynchites bicolor* Fabr." This is obviously a confusion of facts about two species of snout beetles.

The description of the adult seems to refer to an *Attelabus* sp., which lays eggs in small nests made by the female on leaves of trees, including oak. The statement that the beetle frequently punctures the ripe fruits of blackberries and raspberries, causing them to decay, presumably refers to *Rhynchites bicolor*. But the assertion that "this beetle is very destructive to grapevines" in portions of Europe does not apply to *Rhyn. bicolor*. Chittenden (1901) quoted Craw on the injury to blackberries and raspberries as having been done by *Rhyn. bicolor*.

Adult: food and damage. The western forms of *Rhyn. bicolor* include a wider variety of rosaceous plants in their dietary than do their eastern relatives. While roses appear to be the principal food, and thereby suffer the greater injury, related plants of the genus *Rubus*, also are sometimes utilized and injured. The curculio is known to attack petioles, leaf buds, flower buds, flowers and their expanded petals and fruits of both *Rubus* and *Rosa*. However, some of the reports do not specify the parts eaten or the nature and extent of the resulting damage.

When associated with roses, the adult western *Rhyn. bicolor* appears to prefer the buds, boring holes into them, with the consequence that the petals do not open. Robertson (1923) counted as many as 20 punctures in a single rose bud. Hoerner (1936) adds that whereas the beetle mostly penetrates only the petals, it sometimes bores through both the petals and sepals of the bud, or even its base. Some punctured buds open, he relates, exposing the riddled petals. Another frequent injury results from cutting the flower stem, or petiole, just below the calyx, so that the buds wilt and die, and drop to the ground. One or more of the above

types of feeding attack are reported by Lovett (1915) for Oregon, Robertson (1923) for Manitoba, Hoerner (1936) for Colorado, Riley and Howard (1891) and Cockerell (1894) for New Mexico, and Chittenden (1901) for Montana, New Mexico and California.

According to Lovett (1915), leaf clusters are taken as food in Oregon. Hoerner (1936) adds, regarding the use of vegetative parts of the rose, that young shoots may be eaten off, or the stem punctured so that the tips will curl and dry, when flower buds are not plentiful. The newly emerged young beetles usually began feeding on young growing tips of the rose shoots, eating the tender leaves or stems, or the rose buds. Then as the flower buds on the early varieties became scarce the beetles fed on later varieties.

Little notice is given in the published reports to feeding and injury to rose hips; perhaps for the reasons that some of the western varieties of the rose curculio may not oviposit in hips, hence do not puncture them, and that the achenes have had little commercial value because of infrequent use in propagation of roses. Lovett (1915) recorded that the curculio punctured rose hips in Oregon.

The injuries to roses by the adult curculio may have serious consequences for the grower of roses. Comments from the literature are cited to this effect. In Montana, the beetle was the cause of numerous complaints from rose growers in 1923 and 1924 (Cooley, 1903, 1925). At Santa Fe, New Mexico, it was "very troublesome" about 1894 (Cockerell), and in Manitoba it did considerable damage to roses about 1923 (Robertson). Hoerner (1936) states that the damage by *Rhyn. b. wickhami* was so severe in some sections of Colorado for a number of years that it was almost impossible to grow roses out-of-doors.

That intensity of natural light affects the amount of injury by the beetle was observed by Robertson (1923). The wild roses, *R. blanda* and *R. acicularis*, growing under trees were infested by the curculio to the extent of 29.6 per cent, whereas when growing exposed to more sunlight, 60 per cent were infested.

When associated with species of *Rubus*, western varieties of *Rhyn. bicolor* feed in the same manner and on the same parts attacked when feeding on *Rosa*; namely, leaf buds, flower buds and stems, or the berries. Mentioned in this connection are raspberry and blackberry, and their hybrid loganberry, and thimbleberry, with the first two cited most frequently and widely. Specific instances are: injury to blackberry in Colorado (Cassidy, 1888); serious injury to blackberry, raspberry and thimbleberry sometimes done in Oregon (Zeller and Schuh, 1944); and ripe fruits of blackberry and raspberry punctured, causing them to decay in California (Craw, 1894). Lovett (1915) describes the injury to blackberry more fully, for Russellville, Oregon. One to several beetles oc-

curred on almost all clusters of flower buds, and affected one-half to two-thirds of them, causing them to turn brown and die as a result of numerous "feeding and egg punctures." Also the stems for a short distance below the bud were dead, and the buds drooped over. In Manitoba, injury to blackberry and raspberry was negligible (Robertson, 1923). Hoerner (1936) did not find *wickhami* feeding on raspberry in nature, but the beetle ate the buds when no rose buds were available in cages.

Mating, fighting, and locomotion. Mating occurs at any time of the day, and each male and female may mate several times with different individuals (Hoerner, 1936). This observer, on several occasions, also saw males fighting, raising their beaks above their opponents and bringing them down with considerable force. When disturbed, the adults draw their legs to the body, depress the beak, and thus usually fall off the plant, where they lie motionless for a time. Cooley (1903) observed that the beetles are shy and soon disappear under a leaf or stem when a person approaches. Lovett (1915) described them as very sluggish, dropping readily when their activity is interrupted.

Oviposition and larval life. The accounts of these activities of *Rhyn. bicolor* in the west differ particularly with reference to the parts of the host plant wherein the egg is placed and the larva feeds and develops.

In Montana, Cooley (1903) found the eggs placed in various parts of the rose plant. Most of them were either in the unexpanded petals of the flower bud, or in the young fruit. He also discovered an egg in the tender extremity of a new rose cane, and one in a cynipid gall. Presumably the gall grew on the rose plant. In all cases the eggs lay in the holes made with the beak, and well below the surface. A hip that contains an egg "shows a blackened scar on the side which marks the spot where the parent beetle bored in to deposit the egg." He observed also that the beetle bored holes into the stems at right angles to the axis, causing the buds to wilt and dry, and hang from the stems. I quote Cooley's next statement in full below because it emphasizes what appears to be a distinct difference in the larval niche of this insect in Montana as compared with that of the larva in some other areas of the northwest.

"We have not been able to see any particular significance in the boring of holes into the stems, though when we began the studies, it was thought possible that the buds were caused to wilt and dry for the purpose of preparing a suitable food for the young. Though very many such buds have been broken open and examined, we have never found a larva feeding in one." Later in the article Cooley added the following about the larva. "We have never been able to find larvae except in the rose hip or fruit, and this is doubtless the normal place for their devel-

opment . . . They feed upon the seeds which fill the greater part of the cavity of the fruit. The fleshy coating of the fruit is not eaten so far as we have observed. Examination of a fruit containing a nearly full-grown larva shows a part or all of the seeds excavated to mere shells and the body of the larva buried in a mass of waste and excrement."

Lovett (1915) seems to have made no search for the eggs and larvae in punctured rose buds, but did discover that "the larvae feed in the seed pods," "devouring the seeds and leaving little but the shell."

According to the report by Robertson (1923) for Manitoba, the eggs of *Rhyn. bicolor* are placed in punctures in buds of roses, generally one to each bud. The resulting larvae "live for a short time within the flowers and then go to the hips, where they are found in late August feeding on the seeds."

Hoerner (1936) has given us the most complete account of the process of oviposition and larval life. The curculio bores "egg punctures" in the flower buds of roses, and deposits the eggs into the punctures. She likewise punctures the stem that supports the bud, causing both bud and stem to wilt and die.

The eggs were found deposited at various depths from just beneath the surface to about 2.0 mm. below the surface of the buds. The eggs sometimes lay under the outside petal; again under four or five petals. A few had been placed inside single petals. With wild roses, or in buds with few petals, the eggs may be introduced directly among the stamens. Rarely, the eggs occur in the base of the bud; all the rest were in folded petals, but here no definite position seemed to be preferred. Rarely more than one egg is found to have been deposited in a bud under field conditions.

When the egg has been placed into the puncture, the opening is invariably plugged with bits of petal chewed off the edges of the puncture, as Hoerner has observed, and can then seldom be detected except as a slight scar, or sometimes as a small protuberance on the bud, or swelling on a petal.

As observed by Hoerner (1936), the actual number of eggs laid varied from 16 to 143 per female; the average number deposited by 64 individuals was 37. The largest number laid by one female in 24 hours was 8.

The larvae of *Rhyn. b. wickhami* hatch and develop to maturity within the dead rose buds as these either hang on the bush or lie on the ground. Under natural conditions, the small larvae are in most cases found among the stamens, and, Hoerner states, pollen probably is their main food when they are first hatched. "Later, when the larvae become two-thirds or almost full-grown, they are practically always found in the base of the dried bud."

The discovery, by Lovett (1915), of eggs in the buds of blackberry suggests that *Rubus* may be a second host of a western variety of the rose curculio. However, his observation that "the young grubs did not feed at all" in the buds, leaves the question of hostship open to doubt. More thorough investigation is indicated.

Summary: oviposition and larval life. Western forms of *Rhyn. bicolor* usually place their eggs either into the flower buds of rose, or into the rose hip, and larvae variously inhabit the buds only, the hips only, or both buds and hips. For example, Robertson states that the eggs are placed in the bud, where the larvae reside for a time, then move to the hips. Cooley reported finding eggs in the "unexpanded petals," or rose buds, but larvae only in the hips. The careful studies by Hoerner revealed both eggs and larvae are confined to rose buds. Moreover, both eggs and larvae of the eastern *Rhyn. bicolor* have been found only in the hips of roses.

Thus we have a graded series of variations with reference to the specific sites of the eggs and the larvae. This condition suggests more investigation to determine whether the observed variations, and possibly others still remaining unknown, may be correlated with forms of the rose curculio. The bionomic facts already at hand may justify recognition of two or more species in the taxonomic entity now treated as *Rhynchites bicolor*. Such a division was indicated by Green (1920) on the basis of certain structural differences noticed among western varieties.

Behavior of the mature larva. The earlier observers, Cooley (1903) and Lovett (1915), learned that the full-grown larvae leave the rose hip. Cooley's discovery of openings in hips that no longer contained larvae indicated to him that the larvae "eat out of" the hips and go to the ground. But his supposition that they pass the winter as pupae has since been shown to be in error. Also, Lovett concluded that they leave the hips when he found in late August and September that the inner portions of the "seed pods" had been devoured and the invaders had disappeared. Robertson (1923) stated positively that the mature larvae bore their way out of the hips, fall to the ground and bury themselves about 1.5 to 4.0 inches below the surface of the soil, where they hibernate. Hoerner (1936) learned that the mature larvae "leave the buds and enter the ground, where they pass the winter in small earthen cells about 6 mm. in diameter and about $\frac{1}{2}$ to 2 inches below the surface. Larvae were dug up from the soil beneath rose bushes in October, November, February, March, April and early May." By this means, he proved that the matured larvae constitute the wintering stage of *Rhyn. b. wickhami*.

Pupation. Cooley (1903) and Lovett (1915) were unsuccessful in finding the pupae because they looked for them in the fall season. Robertson (1923) stated that pupation begins in the middle of May in Manitoba. Hoerner found pupae in the earthen cells made by the larvae in the ground. "They habitually lie on their backs, and can move around quite readily in their cells by means of abdominal movements, aided by the caudal spines." By about the second day of pupation, the compound eyes show as brown spots on the otherwise white pupa, and in five or six days more the eyes, mandibles, tarsi and caudal spines become light brown. These, and other parts, gradually darken until the mature adult state is reached.

Emergence of the adult. To determine the age of the adult beetle before it works its way from the pupal cell to the surface of the ground, Hoerner (1936) secured pupae that were about ready to transform into adults. He placed them in the bottom of a small glass vial, covered with a pupal cell and an inch of dirt. Thus he learned that "it takes the adult four or five days to become fully colored and hardened, and a day or two to work its way to the surface." The beetle appeared unable to emerge through dry soil, but worked its way out in a day through moistened soil, and began feeding soon thereafter.

Life cycle. The data supplied by investigators of the western forms of *Rhyn. bicolor* agree either in indicating, or in stating expressly, that this species has one generation in a year. However, Hoerner (1936) dug a few mature larvae from the ground in April which did not pupate as expected but persisted all the following summer and winter as larvae. Thus, some individuals of the western forms, like their eastern relative, may enter upon a larval diapause of unusual duration.

In Montana, Cooley (1903) observed that the beetles appeared on rose bushes early in June, and continued there until the latter part of August. He estimated that the egg stage lasts about 7 to 10 days, and speculated that the emerged larvae leave the hips and go into the ground, transform to pupae, and pass the winter as such. But he probably erred in regard to the stage of wintering.

Near Russellville, Oregon, Lovett (1915) found the adults abroad and ovipositing in flower buds of blackberry on May 27, 1912. He made several unsuccessful attempts to work out the life history, and therefore gives the following "approximate life history." The adults are present and active from late spring until late summer and early fall. Eggs were found from May until late July. "The egg stage is about twenty days." Larvae from very small to full-grown sizes were found in rose hips in late August and September, while larvae matured and emerged from others in the same period of time. Although Lovett failed to find pupae

at this time, he predicted that the adults emerge in spring from overwintering pupae. On the basis of his incomplete knowledge, he believed the species to be "single-brooded" in Oregon.

In Manitoba, Robertson (1923) noted that the adults begin to appear in the early part of June, and are most abundant at the middle of this month. Hatching of the embryos begins in the second week of July. The larvae, which first feed within the flowers, are found in the hips in late August. From about the fourth of September, the larvae bore their way out of the hips and enter the ground, where they hibernate. In the middle of the next May, pupation begins, and after two weeks the first adults emerge to appear on the rose bushes. These facts indicate one generation per year in Manitoba.

Hoerner (1936) showed that *Rhyn. b. wickhami* has one generation in a year in Colorado. His findings cover a number of bionomic features of the rose curculio for which no data were previously available.

The adults emerge from the ground during the latter part of May and the first part of June. The average length of life of the emerged beetles was found to be about 7 weeks; 109 individuals lived an average period of 41.78 days. Males lived longer than females, or an average of 43.06 and 40.72 days, respectively. Two females lived the unusual period of 97 days.

Embryonic development required about 10 days, but the period varied considerably with environmental temperature. In the latter part of May, the eggs hatched after about 11 or 12 days; in the warmer weather of July, they did so in 8 or 9 days. The extreme periods of incubation were 8 and 15 days, the average 10.47 days. However, it appears that some factor in addition to atmospheric temperature helps to determine the duration of incubation, for Hoerner found that eggs deposited on the same day varied as much as four days in the period required for embryonic development. The mouthparts, especially the mandibles, of the embryo can be seen moving inside the chorion about 36 hours before hatching.

By exposing rose buds to laying females for a day and keeping these buds until the larvae emerged from them, Hoerner obtained values of 93 and 142 days for the developmental period of the larva. Inhabited buds collected in the field in early summer yielded mature larvae from July 16 to October 6. These facts were taken to indicate that the growing phase of the larval period may be as short as 45 or 50 days. Hoerner (1936) showed that in Colorado also the mature larvae pass the winter, since he dug them from the soil beneath rose bushes, between October and early May. Hence, the over-all life of the full-grown larvae may extend from July of one year to May of the next.

Pupation required about 9 days in April and early May in Colorado,

and the resulting adults emerged from the ground about two weeks later, in late May and the early part of June.

NATURAL ENEMIES OF *Rhynchites bicolor* (FABR.)

To date I have only one reference to natural enemies of the rose curculio from the literature. This pertains to an ichneumonid determined by R. A. Cushman as a species of *Temelucha*. Hoerner (1936) found it parasitized three per cent of the larvae of *Rhynchites bicolor wickhami* in Colorado.

In the course of my investigation of *Rhyn. bicolor bicolor*, five species of hymenopterous parasites were reared. The most numerous of these was the ichneumonid, *Luchatema baldufi*, a solitary endoparasite confined to the larval host. The lesser four were solitary ectoparasites on the larvae. These comprised two species of the family Braconidae, *Bracon mellitor* and *B. variabilis*, and two Chalcidoidea, *Zatropis rosaecolis*, and *Eurytoma* sp.

I have also obtained specimens of an oligochaete annelid, determined by Dr. L. J. Thomas, University of Illinois, as a species of *Chaetogaster*. These were associated with immature stages of the rose curculio unearthed from soil pots at Urbana. Dr. Leland Shanor, then mycologist, University of Illinois, cultured the fungus *Beauveria globulifera* (Speg.) Pic from mature larvae of the curculio which I submitted to him for study. Mites of the species *Caloglyphus spinitarsus* (Herm.), Acaridae, were commonly present in soil pots that housed larvae and pupae of the rose curculio or contained the meconia of *L. baldufi*, but performed in the role of scavengers.

Luchatema baldufi Walkley, Ichneumonidae, Hymenoptera

In the years 1946 to 1951, inclusive, I accumulated a series of 151 adults—62 males and 89 females—of this parasite. Most of them were reared from the larvae of *Rhynchites bicolor*. A smaller number of them were captured on rose bushes in Urbana. In addition to these, the collection of the U.S. National Museum contained a number of specimens accumulated in previous years. Luella M. Walkley (1956), specialist in the Ichneumonidae at the National Museum, found that the above materials represent "a genus and species of Tersilochini new to the described Nearctic fauna."

Distribution. The specimens in the national collection originated in Massachusetts, New York, Iowa and South Dakota. Those obtained in Massachusetts were taken from flowers of *Physocarpus*, *Rubus*, and *Hydrangea* grown in the Arnold Arboretum, Boston. This observation

indicates the adults feed on pollen and nectar. To date, the larva of the rose curculio, *Rhyn. bicolor* is the only known host. Here it is a solitary endoparasite. I have reared the species from the rose curculio contained in rose hips available to me in Urbana from Saskatoon, Saskatchewan; Mapleton and Mt. Timpanagos, Utah county, Utah; Ely, Minnesota; Solon Springs, Chetek, Rice Lake, Black River Falls, Endeavor and Madison, Wisconsin; Crete, Nebraska; Rochelle, San Jose, Bath, Velma, Rising, Mahomet, Urbana, Mayview, and Philo, Illinois, and Jamestown, Indiana.

The above records indicate a wide distribution of *Luchatema baldufi* over the northern United States and southern Canada from at least the Rocky Mountains to the Atlantic Ocean.

Adult (Fig. 39). The distinctive characteristics given here are from Miss Walkley's original description of the species. Only enough characters are selected to distinguish the adult from other Ichneumonidae reared from rose hips.

Length of females, 4.3 to 7.0 mm.; males, 4.2 to 7.0 mm. Body black, except clypeus, mandibles, palpi, legs, abdomen and ovipositor, which are reddish brown, with the antennae, legs, mandibles, clypeus and mouth parts more testaceous. Head transverse, broader than long and broader than thorax. Thorax at least seven-eighths as high as long, polished, pubescent, and finely but densely punctate; hind basitarsus nearly as long as remaining tarsal segments combined. Abdomen polished, lacking pubescence, with long slender petiole about two-thirds length of thorax; ovipositor about as long as body, slender, upcurved, sheaths blackish with reddish tinge, slender, sparingly hairy and ridged.

Through the day and until sunset, I have seen adults on wing, zig-zagging at a fairly fast speed among the tops of the rose hedges on the campus at Urbana. Now and then they alighted to crawl over leaves and hips as if exploring for prospective hosts. On some short visits to the hedge, seven to nine individuals were seen in June. Mating and feeding were not observed.

Oviposition. Although always alert to discover the females engaged in oviposition, I witnessed this procedure only once. The sun had just set on July 4, 1949, at Urbana. This individual clung with her legs to a rose hip that bore an egg puncture of *Rhynchites bicolor*. The three pairs of tarsi were set close together, not spread widely, and the body stood out almost vertically from the hip over the egg puncture. The terebra, withdrawn from its sheath, was held parallel with the venter of the body and directed cephalad so it extended straight into the egg pit. Then the abdomen vibrated vigorously sidewise while bringing pressure on the terebra as it bored into the pit. About one minute was spent in

drilling into the puncture, after which she remained quiet for a few seconds, while the egg presumably passed through the terebra into the host. The terebra was then withdrawn and replaced in the sheath.

In less than a minute, this adult repeated the above ovipositional process on a second egg pit on an adjacent hip 1.5 inches from the first. The two operations combined required 4.5 minutes.

The two hips concerned here were dissected 1.5 hours later. Each contained a first instar of *Rhynchites bicolor*, and each larva inclosed a whitish, smooth, apetiolate egg about 0.35 mm. long with no trace of embryo. The form is shown in Fig. 44. In each larva, the egg had been inserted into the body cavity. These, and other eggs of this parasite, discovered while I dissected other host larvae, lay unattached among the viscera of the host, from which they were readily disentangled, and sometimes popped out when the host's body wall was opened. To check on the possibility that the egg may be inserted into the host egg, I dissected also eggs of the curculio during the season of parasitization. All results were negative.

If *Luchatema baldufi* paralyzes the host incident to oviposition, the inactivating effect is of short duration and slight intensity. The above larvae were normally active 1.5 hours after parasitization.

Host instars attacked. Discovery of parasite eggs in many small larvae of the curculio dissected has caused me to believe that mostly first and some second instars are attacked by the ovipositing female. It is very likely that selection of these instars is determined by their location at or near the inner end of the egg pit of the curculio. In other words, these prospective hosts lie in a direct line with the egg pit where the terebra is certain to strike them when it is inserted into the hip. More advanced larvae are likely to escape parasitization for the reason that they move from the egg site as they feed and grow, thereby reaching a location that is out of line with the introduced terebra.

Reproductive capacity. Indications of the capacity of *L. baldufi* were obtained from dissection of a gravid female taken in nature on June 20. Each ovary consisted of 18 ovarian tubes. Each tube contained nine eggs sufficiently developed to permit identification. Thus, this individual was potentially capable of inserting 324 eggs into host larvae. Moreover, some eggs may have been deposited before the female was captured, and others might have developed had she been permitted to live. Since the species is proven to be essentially solitary, two eggs per host being infrequently found, the potentialities for reduction of the host population by a single female may exceed 400.

Each ovary has a cup-shaped egg calyx at its base and is joined to the median oviduct by a slender lateral oviduct almost as long as an

ovarian tube. The fact that the ova did not swell while they lay in cold water for a half hour indicates an impervious chorion.

Larval instars. On July 4, 1949, I found a larva of the parasite with its caudal process still enveloped in the broad end of the chorion. The parasite then was about 0.35 mm. long.

How many instars compose the larval stage of this *Luchatema* was not determined. But, like many other endoparasitic Hymenoptera, the present species has a very distinct first instar, both structurally and bionomically. The fact that this instar occupies about nine-tenths of the annual lifetime of its species, accounts for the relatively large amount of data presented below concerning it, as compared with that for subsequent instars.

I first became aware of the unusually prolonged first stadium in 1943, while investigating the rose seed chalcid, *Megastigmus nigrovariegatus* at Urbana. Incidental to that study, I discovered what were obviously first instars of a Hymenoptera species in larvae of the rose curculio in hips of *Rosa rugosa*. Dissections were continued all that summer in the hope that the advanced forms of the parasite would be found. But only first instars were present. It was not until the spring that the adult, required for specific identification, was reared. That this is the normal course of development in this species has been confirmed again and again in subsequent years.

When newly hatched in the body cavity of the host, this slender, apodous caudate parasite is about 0.35 mm. long and one-eleventh as wide (Fig. 40). From July to October, it grows to a maximum length of approximately 2.0 mm., with a comparable diametrical enlargement (Fig. 41). In the early developmental phase of the instar, the bases of the head and caudal process are as broad as the thorax and abdomen; but as the instar grows, these anterior and caudal parts distend but little, whereas the intermediate region enlarges from 3.0 to 3.5 times, yet remains almost cylindrical in shape. Thus, in its advanced or mature phase, this turgid instar resembles a rolling pin in form, with the narrow head and the caudal process representing the handles.

Excepting these changes in sizes and form, the first instar possesses essentially the following structural characteristics throughout its life: head pale brown, sclerous, about 1.5 times longer than thick, with minute subterminal ventral mouth parts; postcephalic parts white; thorax and abdomen (exclusive of caudal process) moderately depressed, subcylindrical, and about uniform in diameter, composed of 13 segments which vary little in size, and each constricted transversely at the middle so it appears double; particularly distinctive are the two pairs of udder-like, fleshy pseudopods, one pair on the ultimate abdominal segment, the other on the penultimate segment; the pseudopods appear to be at-

tached to the outer ventral edges of the segments, and are capable of elongation and shortening; abdomen terminates in a fleshy but subrigid, tapering, downcurved process; on the dorsal side, at the base of the caudal appendage, is a marginal notch, beneath which the blind hind intestine terminates.

In addition to the small to larger spheres of yellow food substance, the mid intestine infrequently contains bubbles of gas. In one such case, a first instar 1.5 mm. long contained three largish bubbles amid the golden food in the posterior half of the tract.

The slender form of the first instar seems well adapted to move freely among the semifluid viscera of the host. But if one may judge from observations on larvae in water, their movements are largely nonlocomotor. The extent of these activities varies decidedly with the degree of bodily dilatation; in its younger slender phase, the instar is flexible and changes posture easily, but as it becomes more and more distended during growth, it becomes less agile, more turgid and stiff, and eventually tends to be lethargic and motionless until disturbed. In the later, less active phase, the specific gravity decreases to the extent that the larva, newly removed from the host, floats lightly on water. This condition facilitates finding the parasite among the viscera of the dissected host.

From the normal linear posture, the young flexible instar commonly assumes two other positions. In one instance, it turns the cephalic and caudal ends sharply and quickly dorsad, thereby taking the form of a capital letter U, but with the caudal process raised higher than the cephalic end. It also goes easily into the shape of an attenuated letter S, and may simultaneously roll over and over sidewise in a brisk manner. It is especially while the larva performs the lateral roll that the abdominal pseudopods are elongated and projected to be best seen, although only for an instant.

Growth of first instar. The larva of *Luchatema baldufi* remains a first instar from early summer of the year it hatches from the egg until late spring to mid-July of the next year, or as long as a year to 13 months. During the period indicated above, it undergoes two functionally distinct phases—feeding-growing and diapausing. First instars totaling 461 removed from host larvae of various ages showed growth from 0.35 mm. at hatching in June and July, to 1.3 to 2.2 mm. in length during mid-August to November. The first mature hosts emerged from hips about mid-August, the last so late as early December, in Urbana. The parasites of the larger sizes, and removed from hosts in the later months, had completed their growth, and assumed the form of a rolling pin. This range in size does not signify varying degrees of immaturity, for larvae of like variations occurred in the hosts during the ensuing months of winter, spring and early summer, i.e., to the time of their first molt.

Persistence of mature first instars through three seasons indicates they have entered diapause of an intense character that is probably induced by some inherent physiological factor.

The first instar appears to persist in the diapause so long as the fat body of the host retains the form of whitish slabs normal to all the instars. The normal disintegration of the fat body into the puréed state appears to coincide with the advent of prepupation. The breakdown of the fat body and the first molt of *Luchatema* may therefore prove, with more intensive study, to be precisely concurrent events and actuated by one and the same causative agent—possibly the pupational hormone of the host.

The unusually prolonged feeding-growing phase of this parasite has prompted me to suggest what may be the cause. Since the mouth parts are obscure and inoffensive, they, along with the nature of the food ingested, may explain the slow growth. During its entire feeding phase, the instar seems to ingest the yellow blood plasma of the host, and small globules of free fat. Small amounts of the plasma flow from all host instars when their body walls are punctured. The voluminous white semisolid slabs, which fill the mature host larva snugly, appear at no time to be disrupted by the parasite, and the nature of the substance present in the digestive tract indicates it ingests no fat body. If so, the fluids the parasite swallows may be so small in amount and so lacking in nutritive value that growth can be made only at a slow rate.

Advanced larva. The development of the parasite from the time of its first molt to its full-grown state is certainly relatively brief, for it requires only a few days as compared with the 8 to 12 months devoted to the first stadium. This surprising acceleration in rate of growth may perhaps be due to two further developments in the host-parasite relation. These are the more simplified but efficient suctorial mouthparts of the advanced parasite, and the puréed state of the adipose of the host. These modifications appear to combine to accomplish a single result, namely the quick voluminous transfer of the host's inner substance into the gut of the parasite. In this way, the parasite quickly attains its full size while the host is killed as it is robbed of its large bulk of creamy, homogenized fat body.

The number and distinctive characteristics of the advanced instars of *Luchatema baldufi* have not been determined. As the larva progresses from the second instar to the last, it increases in length from about 2.0 to 5.5 mm. (Figs. 42, 43). The body is then elongate-oval, its plumpness or form varying with the amount of food previously ingested; more or less depressed or sagged, both ends blunt, the prominent caudal process of the first instar now greatly reduced to lacking; head white like thorax and abdomen; body appears 13-segmented until dilatation from feeding

obliterates the intersegmental folds; cuticle of some larger larvae bare, shiny, finely wrinkled, while that of others appears finely granulated; these differences in sculpture may indicate two separate instars. On a larva 2.0 x 5.5 mm., I observed a small tubercle, probably spiracular, on the anterior half of each pleuron of segments 4 to 11. Small white subcuticular speckles of adipose visible externally on living larvae also probably indicate the last instar. The two pairs of pseudopods present on the abdomen of the first instar have not been seen on the advanced larvae.

Cocoon, pupa and emergence of adult. The cuticle of the dead host is filled snugly by the full-grown parasitic larva and is then papery and fragile so that it is readily sloughed off as a crumpled mass. This lies in the posterior end of the host's cell in the ground in late spring. Now the parasite proceeds to spin its cocoon. These events mark the beginning of the prepupal stage, during which the parasite retains its external larval form while the external aspect of the pupa develops within.

The cocoon (Fig. 45) generally fills the host's cell completely and therefore reflects approximately the form and size of this cell. In the period of May 30 to July 19, 1951, I measured 136 new cocoons, whose hosts originated at Chetek, Wisconsin. Their average length was 5.24 mm., their average maximum diameter 3.19 mm. The two smallest cocoons measured 4.4 x 2.2 and 4.2 x 2.7 mm.; the largest, 6.08 x 3.80 and 6.25 x 4.00 mm. Fifty-eight cocoons that contained female pupae averaged 5.49 x 3.33, while 34 spun by male larvae averaged 4.85 x 2.94 mm. The smallest female cocoon was 4.5 x 2.4, the smallest male 4.4 x 2.2; while the largest were 6.25 x 4.00 and 5.65 x 3.65 mm., respectively. The measurements of the 136 specimens also showed a considerable variation in the ratio of length to widest diameter, i.e., differences in form or shape.

The cocoons consist of two distinct silken layers of different textures, an outer one of dull white loose meshwork, and an underlying one with a smooth inner surface and composed of thin sheets resembling onion skin in texture. Into the outer layer may be woven a transverse median band of whiter silk of variable width, and sometimes also a longitudinal ridge of silk along each lateral surface.

Frequently I found "lifesaver"-like rings of golden color in the wall of the cocoon, especially in the middle of the upper side. At first a cause of perplexity as to their nature and origin, they proved to be droplets of water evaporated from the prepupa and the meconium within. Some were suspended from the inner surface of the cocoon, others enmeshed in the external webwork. They varied in size, and adjacent ones were, by pressure of a needle on the cocoon, caused to merge to form larger drops. They were present in largest numbers when the occupant or material were soft and moist, but few or lacking when the advanced pupa had developed a more impervious cuticle.

The termination of the prepupal phase is heralded by the advent of reddish lunate compound eyes visible through the cuticle on the pupal head within the prepupal pronotum; also by the decided thickening of the abdominal area to an elongate-oval form, and by the elimination of the meconium, this discharge taking place shortly before the ecdysis of the prepupal cuticle. When eliminated, this accumulated waste has the form of a half disc (Fig. 45a), its anterior face flat and the posterior side convex to conform to the posterior inner wall of the cocoon where it lies. It takes various positions, from almost vertical to different degrees of obliquity. It is a dark brown, thick soupy substance when newly eliminated, and the end of the pupal abdomen may become inserted into it. The discharge of this waste leaves the prepupa, and the new pupa, entirely white, excepting the eyes.

Shortly after defecation, the shedding of the prepupal cuticle reveals the pupa. Its head and thorax are at first pure white, excepting the brownish red compound eyes, whereas the abdomen is white tinged with yellow. Particles of adipose are visible through the semitransparent, flexible membranous venter of the abdomen. The sheaths of the ovipositor curve dorsad around the apex of the abdomen and extend forward along the dorsum of the entire body, including the head.

The cocoons were found at various depths; empty cocoons found four inches below the surface indicate that the young adults can emerge from this depth of soil. When cocoons containing fully developed young adults were unearthed and opened, the insects sometimes proved able to use their legs for running, and some also took to wing, although awkwardly, as soon as they were released.

Extent of parasitism. The records involved here were obtained in the years 1946 to 1951, by dissecting host larvae of all instars from several species of roses growing in localities in Saskatchewan, Utah, Wisconsin, Illinois and Indiana. The random sample concerned was processed only during the summer and fall in which the host larvae developed; the parasites were therefore all first instars. A total of 790 individual first instars were discovered in 1888 larvae of *Rhynchites bicolor*. Because multiple parasitism in this case was found to be so infrequent as to be almost negligible, the over-all sample was parasitized to the extent of about 42 per cent.

However, the degree of parasitism varied decidedly as to place and years, as the following instances show: Chetek, Wisconsin, 1946-51, 55 per cent; Madison, Wisconsin, 1946-47, 36; Urbana, Illinois, 1947-51, 42; Mayview and Philo, Illinois, 1947-51, 15; and San Jose, Illinois, 1951, less than one per cent of 417 hosts dissected.

Superparasitism. As defined by Imms (1931), superparasitism is acci-

dental, not obligatory, in the instance of *Luchatema baldufi*. Of 790 larvae of *Rhyn. bicolor* parasitized by first instars, very few contained more than one individual. In five cases discovered, the host larvae had matured and remained alive. In four instances, one of the two parasites remained alive. The four living individuals were first instars, whereas three dead ones were first instars, and the fourth was a second instar, with the exuviae still adhering to the body. In the fifth instance, both parasites were first instars. One living larva measured 1.8 mm., whereas the associated dead one was 0.8 mm. long, and, moreover, enveloped in a large mass of transparent gelatinous substance, possibly phagocytes. Another dead parasite had become greatly inflated, probably by gas of decomposition. None of the dead parasites bore evident marks of injury or loss of form that might indicate cannibalism.

Life cycle. The records on which this account is based were secured by dissecting first instars from host larvae, and by rearing the advanced instars, pupae and adults from hosts placed in pots of soil. The hips concerned here grew at Chetek, Wisconsin, and Urbana, Illinois, and were processed at Urbana.

The approximate period of emergence of young adults from the hibernacula of the host larvae in soil is indicated by records for 1949 and 1951. Thirty-two adults issued between June 28 and July 19, 1951, and 53 between June 24 and August 13, 1949. Accordingly the females are abroad parasitizing the smaller instars of the rose curculio in hips from June to late August. That embryogenesis requires at most a few days, is indicated by the infrequent discovery of eggs in small hosts parasitized by very young first instars of *Luchatema*.

Small, recently hatched first instars were discovered by dissection of host larvae as early as the first week of July. Growing very slowly, these first instars attained their mature state from late summer to October. The mature first instars are then in physiological diapause, which continues through fall, winter and spring while the full-fed, emerged host larva lies in its hibernaculum in the ground. Exuviation of the first instars appears to be concurrent with the prepupation of the host, in the period of approximately early May to early June. Thus, the over-all period of the first instar of *Luchatema* extends from late June of the first year to mid-July of the second involved in the cycle.

The advanced instars complete their development in probably less than a week, and simultaneously, by feeding, invariably destroy the host before it can pupate. Advanced larvae were found in soil pots between May 15 and July 20, 1951.

The parasite was in its pupal form from May 29 to July 19. Adults then emerged between June 24 and August 13—the period when small first and second instars of *Rhynchites* are available for parasitization.

Therefore, like its host, *Luchatema* completes one cycle per year, its successive life stages lagging, timewise, behind those of the host.

Bracon mellitor Say, Braconidae, Hymenoptera

Synonymy and distribution. Of four species of solitary ectoparasites found attacking the larvae of *Rhynchites bicolor* in rose hips, *Bracon mellitor* Say, named and described by Thomas Say (1836), was the most numerous. Subsequently it was placed under the name *Microbracon* (Muesebeck, 1925), and later relocated in *Bracon* (Muesebeck, et al., 1951). In his revision of 1925, Muesebeck showed that the names *xanthostigma* Cress., *vernoniae* Ashm., *anthonomi* Ashm., and *pembertoni* Bridwell are synonyms of *mellitor* Say. The literary sources of these names are given in the Synoptic Catalog, p. 166 (Muesebeck, et al., 1951). According to this catalog, the species occurs in the United States, Mexico and Hawaii. My series of 43 females and 11 males appeared in jars containing rose hips from Chetek and Madison, Wisconsin; Ironton, Missouri; Crete, Nebraska; Fox Ridge Park and Kickapoo Park, Illinois, and San Jose, Philo and Mayview, Illinois.

Hosts. Species of *Bracon* prefer hosts from which the ovipositing adults are "separated by an inert covering" (Salt, 1931). In its relation to *Rhynchites bicolor*, *B. mellitor* conforms to that pattern of behavior. Entomological publications show that *mellitor* has also been reared from numerous other hosts of like habits in the Coleoptera and Lepidoptera. The names of the hosts, with the literary sources, so far as known to me, follow herewith.

COLEOPTERA

CURCULIONIDAE

Anthonomus grandis Boh. (Carpenter, 1944; Fenton and Dunnam, 1929; Folsom, 1936; Hixon, 1935; Hunter and Hinds, 1904; Marlatt, 1933; Miller and Crisfield, 1930; Muesebeck, 1925; Muesebeck, Krombein, Townes, 1951; Pierce, 1908; Smith, 1936; Strong, 1934, 1935).

Anthonomus albopilosus Dietz (Pierce, 1908; Muesebeck, 1925; Muesebeck, Krombein, Townes, 1951).

Anthonomus eugenii Cano (Muesebeck, 1925; Muesebeck, Krombein, Townes, 1951).

Anthonomus fulvus Lec. (Muesebeck, 1925; Muesebeck, Krombein, Townes, 1951; Bigger, 1931, 1933; Satterthwait, 1946, 1948).

Anthonomus signatus Say (Chittenden, 1893; Muesebeck, Krombein, Townes, 1951).

Anthonomus squamosus Lec. (Pierce, 1908; Muesebeck, 1925; Muesebeck, Krombein, Townes, 1951).

Desmoris scapalis Lec. (Pierce, 1908; Muesebeck, 1925; Muesebeck, Krombein, Townes, 1951).

Desmoris constrictus (Say), (Satterthwait, 1946; Muesebeck, Krombein, Townes, 1951).

Hypera nigrirostris (Fabr.), (Underhill, 1924; Muesebeck, Krombein, Townes, 1951).

Coeliodes inaequalis Say (Brooks, 1918).

Cylas formicarius elegantulus (Summers), (Cockerham, 1944).

Chalcodermus aeneus Boh. (Bissell, 1940).

Tachypterus quadrigibbus Say (Hammer, 1936).

Conotrachelus nenuphar Harris (Quaintance and Jenne, 1912).

LEPIDOPTERA

AEGERIIDAE

Aegeria scitula Harris (Underhill, 1935).

GELECHIIDAE

Anarsia lineatella Zell. (Basinger, 1935).

Frumenta nundinella (Zell.), (Montgomery, 1933; Muesebeck, Krombein, Townes, 1951).

Pectinophora gossypiella Saund. (Bridwell, 1920; Willard, 1927; Ohlendorf, 1926; Muesebeck, 1925; Muesebeck, Krombein, Townes, 1951).

OLETHREUTIDAE

Crocidosema lantanae Busck (Bridwell, 1920).

Cryptophlebia illepida Butl. (Bridwell, 1920).

Polychrosis viteana Clem. (Johnson and Hammer, 1912; Muesebeck, 1925; Muesebeck, Krombein, Townes, 1951).

Cydia molesta (Busck), (Smith, 1928; van Steenburgh, 1934).

Rhyacionia frustrana (Comst.), (Cushman, 1927).

PYRALIDAE

Homeosoma electellum Hulst (Satterthwait and Swain, 1946; Muesebeck, Krombein, Townes, 1951).

Myelois ceratoniae Zell. (Bridwell, 1920).

Pyrausta nubilalis Hübn. (Baird, 1929).

Pyrausta penitalis Grote (Chittenden, 1918).

COSMOPTERYGIDAE

Mompha stellata Busck (Dickerson and Weiss, 1920; Muesebeck, Krombein, Townes, 1951).

NOCTUIDAE

Heliothis obsoleta Fabr. (Bibby, 1942).

Stibadium spumosum Grote (Satterthwait, 1948; Muesebeck, Krombein, Townes, 1951).

Direct evidence that *B. mellitor* attacks the grubs of *Rhyn. bicolor* came in the discovery of a live adult male in a hip of *Rosa carolina* from San Jose, Illinois, in association with much shrunken dead remnants of a larva of the curculio amid feces and pulverized achenes. In a number of other hips from the same locality, I found similar dead remains of the curculio and a few tough cocoons, such as the larvae of *mellitor* are said to spin.

Extent of parasitism. The incidence of *Bracon mellitor* on the rose curculio was generally low, and certainly under one per cent, except at Chetek and San Jose. Where the cotton boll weevil, *Anthonomus grandis*, was the host, investigators agree that this was the most numerous parasite present, but, on the other hand, they concur in the view it does not effect a desirable degree of control. Parasitism of the boll weevil by all species found by investigators caused 8.22 per cent mortality at Madison Parish, Louisiana, in 1932, due principally to *B. mellitor* (G. L. Smith, 1936), and Strong (1936) stated that about 80 per cent of all the parasites reared from the boll weevil in the cotton-growing area were *B. mellitor*. In Georgia, the average parasitism by *mellitor*, in 1930, increased from 10 to 18 per cent in bolls in June, to 35 per cent in squares on the plants in August and September (Miller and Crisfield). In 1904, 24.4 per cent of 5,548 squares collected in Texas produced adult weevils, but only 1.3 per cent of the population was parasitized, 90 per cent by *Bracon mellitor* (Hunter and Hinds). Miller and Crisfield (1930) also reported an observation, in which Pierce, Fenton and Dunham, and Folsom concur, that parasitism by *mellitor* in bolls and squares on the plant is higher than in fallen ones.

Bracon mellitor occurred in 65 per cent of the heads of sunflower (*Helianthus*) examined by Satterthwait (1946) at Lovington, Illinois, where it parasitized *Anthonomus ("Desmoris") fulvus*. Bigger (1933) reported that 80 per cent of the parasites reared from the same host insect and plant in 1928 to 1932 were *B. mellitor*. However, the highest rate attained was only 6.2 per cent, in 1929. When attacking the oriental fruit moth, *Cydia molesta*, *B. mellitor* constituted only 0.4 per cent of the parasites reared in Michigan in 1930 to 1932 (Merritt, 1933), and was obtained from that host only in small numbers in Ontario, in 1926 and 1927 (C. W. Smith, 1928). Willard (1927) considered it the most valuable parasite against the pink bollworm (*Pectinophora gossypiella*) in Hawaii, yet only 2.33 per cent of this host were parasitized by it in 1918 and 1919.

Adult life. The adult is fairly robust, with dusky filiform antennae, shiny reddish brown head and thorax, orangish yellow abdomen, prominent pterostigma, venation typical of the family. The female bears sturdy

sheaths around the terebra, which is about two-thirds as long as the body. According to Willard (1927), length of the body varies much, depending on the amount of food available to the larva from the host. From small pink bollworms, adults not over 1.5 mm. long have been reared, but the usual length of those developing on this host is 4.0 mm. Similar variations in size have also been reported by other observers; e.g., W. D. Pierce (1908) obtained "a small melanistic form" of *B. mellitor*, which had previously gone under the name *Bracon dorsator* Say.

Willard (1927) and Folsom (1936) showed that the length of adult life varies with sex, food and temperature. "Unfed" males averaged three days of life, and females five days (Folsom). Females fed on water and honey survived 24 to 102 days (Willard), and averaged about two weeks during August (Folsom). After the insects emerge from the cocoon, mating often takes place at once, and may be repeated (Willard). It is, as a rule, performed in 15 to 30 seconds. The procedure is described by Willard. However, insemination is not essential to reproduction. Both Willard and Folsom showed that the progeny of unmated females was invariably male. When Folsom mated these males with females, normal eggs and larvae resulted.

Oviposition. Deposition of eggs usually begins on the second day after eclosion (Folsom), and often not for 5 to 7 days (Willard). The female chooses the place for oviposition by the tactile sense. A cotton square that contains an advanced weevil larva yields to the touch of the terebra because it is hollow. A hard, resisting spot makes the terebra bend, whereas a soft one is penetrable, and an egg is placed here. Since soft spots indicate larger weevil larvae, the parasite chances to prefer large hosts (Folsom).

The attacking female always stings and paralyzes the pink bollworm before she deposits an egg. As the terebra momentarily pierces the cuticle, it injects enough poison to cause paralyzation. After some time, the host becomes capable of only slight movements. An egg is deposited on it as soon as it grows quiet (Willard). According to Fenton and Dunnam (1929), the larvae of the boll weevil are always completely and permanently paralyzed, but not killed at once. The pulse beat slowed in one to 3 days after paralysis. Folsom found the pulse of a normal larva increased with activity from 42 to 60 pulsations per minute, whereas it varied from 24 to 30 per minute after paralysis.

Eggs are commonly attached anywhere on the body, but sometimes to the wall or lint of the host's cell. The egg is pearly white, smooth, attenuated behind, broadly rounded at the head, curved, and 0.866 to 1.256 mm. long. Deposition of eggs required an average of 15.4 minutes during August and September (Folsom). Three confined females laid 116, 121 and 213 eggs, respectively (Willard). Both these investigators

discovered that the females often went through the motions of oviposition, including actual paralysis, without delivering an egg. One female observed by Willard deposited 63 eggs in 4 consecutive days, and later paralyzed 9 larvae on which no eggs were laid.

Some special circumstances have been observed to affect parasitization. The female will not attack host larvae exposed outside the cotton bolls. Squares hanging normally on the plant are parasitized at a higher rate than others lying on the ground in the field. By placing pupae of the boll weevil in cells designed for oviposition, Folsom showed the females can distinguish between pupae and larvae, avoiding the pupae. Carpenter (1944) performed experiments involving *B. mellitor* and the boll weevil, which showed that the number of hosts available to single females affects their productivity. When a female was caged with 20 larvae of *Anthonomus grandis*, the average yield per female was 7.5 adult *mellitor*, but when 5, 10, 15, 30 and 60 females were placed with 20 larvae, the production per female decreased to 2.85, 1.92, 1.47, 0.74 and 0.41 adult *mellitor*, respectively.

Larva. The mature embryo hatches by biting away the anterior end of the chorion with its pointed mandibles. The newly hatched larva is 1.1 to 1.4 mm. long, translucent white, with a distinct head and 13 post-cephalic segments. Willard (1927, pp. 8-11) describes and figures four instars, which are similar and hymenopteriform. The mandibles end in a sharp tip that effectively punctures the body wall of the host.

The young larva travels freely over the smooth body of the cotton boll worm with a crawling-looping movement. It begins feeding by lacerating the cuticle with its pointed jaws, and so sucks fluids from the host. The new first instars may frequently move to new locations on the same host. This travel incidentally brings the parasite into contact with other larvae of its kind that may be present. The resulting combat reduces the number to one, and thereby assures an ample food supply for the survivor. However, two larvae may mature on a large bollworm (Willard).

Only the skin and the head of the boll weevil larva remain when the parasite is full-fed. Differences in size of the host larva are reflected in the "enormous" variation in size of the resulting adult *B. mellitor* (Folsom).

Cocoon and pupa. The cocoon is spun inside the square on the wall of the host's cell. Folsom fully described the process of cocooning. He and Willard give diverse values for the duration of the prepupal stage; these seem to result from their different concepts of this phase of life. The prepupa discharges the accumulated digestive waste within the cocoon. Exuviation of the prepupa requires a few minutes, and the newly exposed pupa is glistening white, except for the reddish brown

eyes. The duration of the pupal stage varies from 3.5 to 5.5 days in temperatures that ranged from 71 to 86° F., in Hawaii. The adult emerges by biting a hole in the end of the cocoon (Willard).

Life cycle. The incubation period averaged 24 hours in August and September (Fenton and Dunnam, 1929), a little less than 24 (Folsom, 1936) and 18 to 28 hours in Hawaii (Willard, 1927). At Tallulah, Louisiana, the feeding-growing period of the larva required only three days, as a rule, but four were sometimes needed in September and October (Folsom). At Florence, South Carolina, development from hatching to cocooning in July and August involved three days (Fenton and Dunnam). Willard determined the duration of the four instars to be 23 to 24, 20 to 23, 28 to 30, and 19 to 115 hours, respectively, in Hawaii. The temperatures varied between 68 and 80° F.

The following differing values given by investigators are attributed to the varied numbers of life phases encompassed by their accounts. According to Willard, the egg, larval, prepupal and pupal periods lasted 28, 187, 28 and 132 hours, respectively, or a total of about 16 days. Fenton and Dunnam found that 10.19 days were required for development from oviposition to eclosion, and Folsom reported the normal period from hatching to eclosion, in August and September, as 12 days. The first three of the 12 days were spent as a feeding larva, the next 6 "as a larva" in the cocoon, and 3 days as a pupa.

According to Folsom, oviposition ended in nature about mid-November, 1934, when frosts killed the weevil larvae in the squares. Some of the cocoons contained living larvae of *Bracon mellitor* in the fall, which indicated the parasite can probably winter as such. My data for *B. mellitor* from rose hips suggest the parasite winters as an adult, and completes its cycle once per year when *Rhyn. bicolor*, a univoltine host, is attacked in Wisconsin and Illinois.

Bracon variabilis (Prov.), Braconidae, Hymenoptera

The taxonomy of this species is treated by Muesebeck (1925; 1951, Synoptic Catalog). The literature contains very little information on its bionomics.

Distribution and hosts. The above references give the distribution of *B. variabilis* as Quebec to Virginia, and west to Missouri and Texas. Other reports have it from Ontario (Garlick), Michigan (Gentner), Kansas (Parker and Lamerson) and New York (Leonard). I have it from Urbana, nearby Mayview and Kickapoo State Park, Illinois. Larvae of Lepidoptera and Coleoptera that develop hidden within parts of plants serve as hosts of *B. variabilis*. From the above literature and other sources cited here, I have the following host records: grape berry-moth, *Polychrosis viteana* (Clem.), Olethreutidae, Pennsylvania; pine tip

moth, *Rhyacionia frustrana* var. *bushnelli* Busck, Olethreutidae; *Blastodacna* sp., Cosmopterygidae; plum curculio, *Conotrachelus nenuphar* Herbst, Curculionidae, Virginia; apple curculio, *Tachypterellus quadrigibbus* Say, Virginia and *T. q. magnus* List, Curculionidae; and an unidentified larva in seed pods of *Oenothera*, Virginia.

The above host records lead me to suppose that, in rose hips, *B. variabilis* parasitized the larvae of *Rhynchites bicolor* and/or *Cydia packardi*. Both these phytophags occurred in the hips of *Rosa carolina* in the localities where my series of eight adults originated. Six of them appeared alive in hip jars between May 15 and June 11, and two on September 10 and 21, in the years 1946, 1947, 1949 and 1951.

Zatropis rosaecolis Burks, Pteromalidae, Hymenoptera

This parasite on the larva of *Rhynchites bicolor* was described recently as a new species by B. D. Burks (1955a) from a series of 3 males and 33 females which I obtained from rose hips in Illinois, northwestern Wisconsin and northeastern Minnesota.

Adult. The adult may be distinguished from other chalcids from rose hips by the following characters taken from the original description by Burks (1955a).

Female—Length 2.0-4.0 mm. Head and body black with faint bluish-green or blue metallic coloration visible from oblique angles; antennal scape yellow or tan, shading to dark brown at apex, flagellum dark brown or black; tegulae and wing veins light brown; coxae black, femora very dark brown with apices yellow, each tibia yellow at base and apex, shaded with brown in the middle. Face clothed with numerous short hairs. . . . Thoracic dorsum with a few scattered, golden-yellow hairs.

“Male—Length 1.5-2.0 mm. Color of head and thorax without metallic sheen.” Dr. Burks comments that *Z. rosaecolis* is the only North American species of its genus which has the face clothed with *simple* hairs and has two rows of bristles behind the marginal vein on the underside of the fore wing.

Distribution and rose hosts. My series of 79 adults, including the above 36 types, consists of 64 females and 15 males. They originated in hips of roses in localities as follows: *Rosa carolina*, Ironton, Missouri; *R. rugosa*, Urbana, Illinois; *R. carolina* at Urbana, Mayview, Philo, Velma, and San Jose, Illinois; *R. Macounii*, Crete, Nebraska; *R. arkansana*, Madison, Wisconsin; *R. blanda* and *R. carolina*, Chetek, Wisconsin; *R. blanda*, Solon Springs, Wisconsin; and *Rosa acicularis bourgeauiana*, near U.S. highway 61, in northeastern Minnesota.

Rhynchites bicolor as host of *Z. rosaecolis*. While dissecting hips of *Rosa carolina* obtained at Urbana, Mayview, Philo and San Jose, Illinois,

and Ironton, Missouri, I discovered five larvae attacking small grubs of *Rhyn. bicolor* in the achene cavities. The inclusive dates were June 16 and August 7. Six small pupae lying adjacent to dead, shrunken, more or less dark larvae of *Rhyn. bicolor* were disclosed between June 9 and August 27. Eleven adults developed from these parasitic larvae and pupae, in the over-all period from June 15 to September 11, through the years 1947, 1948, 1949, 1951 and 1952.

In addition, I discovered 5 adults still enclosed within the achene cavities along with shrunken remains of the host larvae, between July 22 and August 9. These, and the above reared series of 11 adults, constitute positive evidence that *Zatropis rosaecolis* parasitizes the larvae of *Rhyn. bicolor* in the achene cavity of rose hips. It is ectoparasitic and solitary.

Also 61 living adults were found alive in jars of hips grown in areas where *Rhyn. bicolor* is known to occur. The majority of these issued during July to September of the years the larvae developed on the host, but smaller numbers wintered in some undetermined stage in the hips, the adults emerging during May and June of the ensuing year. Since no host stages inhabit the hips during winter, these spring emergers cannot represent a generation distinct from the adults issued the previous year.

The *Zatropis* larva (Fig. 49) spins no cocoon. The mature black pupae lie bare in the achene cavity. My rearing records show that pupation required 7 to 10 days in natural summer temperatures in the laboratory.

That the female *Zatropis* inserts the terebra into the egg pit prepared by the female *Rhyn. bicolor* is indicated by the observations that the hosts are small instars and that these normally remain near the inner end of the pit to feed. Their position here probably renders them susceptible to parasitization.

Eurytoma sp., Eurytomidae, Hymenoptera

Most species of this chalcid genus are black, with the thorax umbilically punctate and pronotum transverse, strap-shaped; abdomen of female compressed and highly polished. Being unusually similar, the species are distinguishable with difficulty, which fact probably explains why many remain unidentified in the literature.

It is possible that two or more species are represented in my series of 22 adults from rose hips. The females vary from 2.1 to 3.5 mm. in length, the males 1.5 to 2.3 mm. Two individuals of the series originated from hips of *Rosa carolina* taken at Chetek, Wisconsin, and 15 from hips of *Rosa* spp. sent to me from five widely separated localities of Iowa in April, 1953. The Iowan specimens emerged from hips between May 7

and 25, 1953; one from Chetek on May 18, and the rest from Wisconsin and from Illinois appeared in hip jars from July to October. This diversity of emergence dates may signify two generations per year in Illinois and Iowa.

I reared a male *Eurytoma* from a newly formed pupa found lying on the dead, dusky shrunken remains of an advanced stage larva of *Rhynchites bicolor* in a hip of *Rosa carolina* at Urbana, Illinois, on August 31, 1947. The adult issued from the hip, in which the pupa lay, on September 9, 1947. The pupal development required about 10 days. In the summer of 1937, I reared another adult from a larva found attacking a grub of the rose curculio in a hip of *Rosa rugosa* at Urbana. These instances form certain proof that my *Eurytoma* sp. at least sometimes parasitizes the larva of *Rhyn. bicolor*. Like *B. mellitor*, it performs as a solitary ectoparasite.

Chaetogaster sp., Oligochaeta, Chaetopoda, Annelida

From September 9 to 24, 1950, I set up a series of 13 cages to house approximately 1,500 mature larvae of *Rhynchites bicolor* that emerged from hips of *Rosa blanda* and *R. carolina* taken at Chetek, Wisconsin, on September 5. The cages consisted of four-inch flower pots almost filled with black soil from my house yard at Urbana. The larvae were the wintering stage of this curculio and were kept out-of-doors in pots countersunk in the ground, from November to May.

Evidence of parasitic life. During May to July, 1951, sample pots were scrutinized at about weekly intervals as a means of determining the developmental status of the beetle and *Luchatema baldufi*, its endoparasite. In the course of examining such a sample on June 17, 1951, I discovered several small, slender, active whitish worms, later determined as an oligochaete annelid of the genus *Chaetogaster* by Dr. L. J. Thomas, University of Illinois. These were associated with a dead, but still fresh, whitish new pupa of the rose curculio in the upper 1.5 inches of the soil. No less than 40 individuals of *Chaetogaster* swarmed from the pupa when it was immersed in well water. They varied from less than 1.0 mm. to 6.0 mm. in length, excepting one 12.0 mm. long. Also on June 15, 1951, a smaller number of such worms was present in another of the 13 pots. These seemed to have scattered into the surrounding soils subsequent to the destruction of the host. No worms were found in the other 11 pots.

Presuming this *Chaetogaster* to be a normal inhabitant of the ground, I concluded that it probably was present in the soil used to fill the pots, or crawled in during the fall or spring when the pots sat in the soil. It seems very unlikely that the parent worm of the aggregation of 40 originated in some rose hip at Chetek. Because the worms found on June 17

inhabited an apparently recently killed pupa, they may be regarded as true parasites.

SCAVENGEROUS MITE

Caloglyphus spinitarsus (Herm.), Acaridae, Acarina, Arachnida

In late June and early July of 1947 to 1951, numbers of this small whitish plump-bodied mite were discovered in soil pots of the type described above under *Chaetogaster*. The pots of soil had been the wintering site of the larvae of *Rhynchites bicolor*, some of which contained the larvae of the endoparasite, *Luchatema baldufi*. In the months indicated above, the eggs, nymphs, and adults of *Caloglyphus spinitarsus* were found in numbers associated with dead larval bodies of the curculio, and also dead bodies and meconia voided in the cocoons of the parasite. The frequent occurrence of many mites in association with these dead organic substances leaves no doubt that the species is a scavenger, not a parasite. I have not found references to it in the *Review of Applied Entomology*, series A. Several congeneric species have been reported there as associated with decomposing plant matter, mushroom culture and corn processing plants, all under circumstances which indicate scavengerism.

THE ROSE SEED CHALCIDS, *Megastigmus* spp., TORYMIDAE, HYMENOPTERA

Most known species of Chalcidoidea perform as entomophagous parasites. Prominent among the phytophagous minority are many members of the genus *Megastigmus*, which have been shown to develop in the seeds of various plants. Two species of the genus are known to develop in rose hips, namely *M. aculeatus* (Swederus) of Europe (Fig. 53), and *M. nigrovariegatus* Ashmead of North America (Fig. 52). Their life histories are similar. Each completes one life cycle in a year—the embryos, larvae and pupae residing in the achenes. The mature larvae are the wintering stage and have a prolonged diapause. Pupation and emergence of the adult occur in the following spring.

The rose seed chalcids are at most 3.0 mm. long, with variable amounts of black and yellow on the body, and particularly on the dorsum. As the generic name signifies, they have a comparatively large stigma on the anterior margin of the fore wings. The females of both species bear long terebras enclosed in bristly sheaths.

Specific differences. These species, although closely related, are for

the most part readily distinguished by the following characteristics I have taken from Milliron's (1946) descriptions.

<i>Megastigmus nigrovariegatus</i> (Fig. 52)	<i>Megastigmus aculeatus</i> (Fig. 53)
A cloudy infuscation surrounding stigma	No cloud surrounding stigma
No black coloration on outer two-thirds of axilla, except on very dark females	Outer two-thirds of axilla black
Ovipositor sheath almost constant in length; distinctly shorter than entire body	Ovipositor sheath distinctly longer than the total body, except in variety <i>nigroflavus</i> Hoffm.

Megastigmus aculeatus (Swederus)

Synonymy. Swederus named and characterized this European rose seed chalcid in 1795, under the generic name *Pteromalus*. In the subsequent 80 years, it was renamed as follows: *Megastigmus transversus* Walker (1833); *Torymus* (*Megastigmus*) *collaris* Boheman (1833); *Torymus punctum* Foerster (1841); *Megastigmus vexillum* Ratzeburg (1848); *Megastigmus flavus* Foerster (1859); *Megastigmus cynorrhodi* Perris (1876). Milliron (1949, p. 289) is my source of this information.

Although obviously not as variable in size and amounts of yellow and black on the body as *M. nigrovariegatus*, the European species, *M. aculeatus* nevertheless displays some variation, particularly as to color. This fact is indicated by Hoffmeyer's (1929) recognition of a variety *nigroflavus*. I share the experience of Milliron in having discovered, among reared specimens, individuals which diverge from the color pattern of both *nigroflavus* and the typical form *aculeatus*.

Food habit. A controversy that engaged the attention of several entomologists in Europe and North America during the nineteenth century was whether *Megastigmus* is "phytophagous" or parasitic. Milliron (1949, p. 355 and forward) gives an excellent account of this historical episode as it pertains to the genus as a whole. Following is an abbreviated statement concerning *M. aculeatus*, in particular.

Two entomological facts about the food habits of Chalcidoidea delayed the acceptance of the phytophagy of *aculeatus*. First, some species of chalcids had early been proved to be parasitic on other insects, and it was therefore generally supposed that all but a few members of the superfamily are parasitic. Second, the larvae of the few exceptional species were found or believed possibly to be of "mixed" or "gemischter" food habit. The early instars of the "mixed" species consumed the small insect host, whereas the advanced instars developed on plant tissue left by the phytophagous host. W. J. Phillips (1927) and Puzanova-Malyshova (1936) describe instances of such mixed habit.

For about 75 years after Swederus named it in 1795, *M. aculeatus* was presumed to be a parasite on some phytophag in rose hips. Because of its larval habitation in the hypanthium and its common occurrence, the European rose hip fly, *Rhagoletis alternata* (Fallén, 1820) was believed to be the host. This view was held, or copied, by Ratzeburg, 1848; Rondani, 1872; Thomson, 1875; Cameron, 1879; Dalla Torre, 1898, and others.

Ratzeburg (1848, p. 182) stated that *M. aculeatus* (*vexillum*) was reared from this fly by P. F. Bouché, but gives no literary reference for the statement. Since Bouché (1833, 1834) does not mention such a host relation, it is likely that the report was received through personal communication, for these men were contemporaries and acquainted.

Reinhard (1857) seems to have made the first observations that cast doubt on the parasitic habit of *aculeatus*. Knowing that the larva of the hip fly leaves the hip in the fall season, he was perplexed when he reared large numbers of adult *aculeatus* from hips collected in winter. Mayr (1874) repeated Reinhard's statement on the dubious parasitic relation.

But especially the studies by Perris (1876) in France, and Wachtl (1884) in Austria, produced evidences that helped to undermine the belief in the parasitic habit. Perris reared many *aculeatus* from hips of *Rosa sempervirens* in the spring season, and, noting holes in the seeds, questioned whether the *Megastigmus* might have inhabited the seeds. Moreover, the hips contained no other insects which might serve as its host. Concluding that *aculeatus* ("cynorrhodi") is more than probably "spermophagous," Perris intended to continue his investigations, but published nothing further on the question.

Wachtl (1884) did more than anyone of his period to reveal the true food habit of *aculeatus* ("collaris"). He reared adults from rose hips and traced their emergence holes from the periphery of the hips to the achenes. No seed at all remained in these, hence the kernel can have been destroyed only by the larvae of "collaris." Later Wachtl found larvae filling the inner spaces of the whole achenes, and no other insects present that may have served as host of the "collaris."

But Howard (1892) and Riley (1893) remained unconvinced and persisted in their opinion that *M. aculeatus* might be a species of "mixed" habits. They cited a number of cases they believed to be mixed. For example, Howard then considered "*Eurytoma funebris*," now known as *Bruchophagus gibbus*—the clover seed chalcid—to be parasitic on *Dasyneura leguminicola* (Lintner)—the clover seed midge. Wachtl (1893) responded to their objection with the declaration that we know only a small fraction of the life of chalcids, and insisted that *M. aculeatus* is phytophagous. He has been supported by Crosby (1909), Milliron

(1949) and others. Moreover, it is the belief of observers today that *aculeatus* confines its life to the achenes of *Rosa* spp.

Few claims to the contrary have been made. Milliron (1949, p. 402) mentions *Evonymus* sp. and *Rhamnus* sp. reported in the literature as food plants of *M. aculeatus*. He regards these as dubious records that stand in need of confirmation. Escherisch (1923) quotes Fuchs (1912) to the effect that *M. aculeatus* parasitized the snout beetle, *Otiorrhynchus sensitivus* Scop., whose larvae feed at the roots of evergreen trees. This is obviously an error.

Distribution and rose hosts. Below I give such records of rose hosts and geographical occurrence as have come to my attention through the literature, together with my own acquisitions. Placed first are those pertaining to the typical form *aculeatus aculeatus* (Swed.); second, those concerned with the dark form that resembles, more or less, the variety *nigroflavus* of Hoffmeyer; and third, records having to do with series not identified as to variety.

I. The typical or light form, *M. a. aculeatus*. In the course of his revisional study of the genus *Megastigmus*, Milliron (1949, 291-92) studied typical material "reared from, or associated with the following species of *Rosa*," and obtained from places named here: *Rosa medwedewii*, Caucasus; *Rosa alpina*, France and Switzerland; *R. rugosa*, Germany and U.S.S.R., and the following from U.S.S.R.—*R. davurica*, *R. jundzilli*, *R. rugosa kamtschatica*, and *R. mollis*. Milliron redescribed *M. a. aculeatus*, from specimens reared from *Rosa* at Jamaica Plain, Massachusetts, and Ithaca, New York. He states it is known to occur also in France, Germany, Switzerland, at Moscow, Gagri and Tiflis, Russia, and in Iran, Peking, China, and French Somaliland, Africa. Nikol'skaya (1934) reported it reared from seeds of *Rosa cinnamomea* in the province of Kuban, North Caucasus, and Poltava, in the Ukraine, of the U.S.S.R.

My series of light-colored specimens were reared at Urbana, Illinois, from hips acquired as follows: *Rosa eglanteria*, Ashe County, North Carolina; *R. canina*, Homeworth, Columbiana County, Ohio; *Rosa*, probably *palustris*, East Liberty, Ohio; *R. eglanteria*, West Lafayette, Coshocton County, Ohio, and *Rosa*, near *canina*, Geneva, New York.

II. The dark form, *M. a. nigroflavus*. Milliron (1949) recorded it from New Jersey; Virginia; Yokohama, Japan; and Saratow, Russia. The types from which Hoffmeyer described the variety were reared at Copenhagen, Denmark, from seeds of *Rosa multiflora* received from Japan. The "New Jersey" record pertains to the series reared by Weiss (1917) from seeds of *Rosa multiflora* shipped from Japan. My dark forms, which approximate the *nigroflavus* Hoffm., originated in *Rosa eglanteria*, Urbana and Kickapoo State Park, Illinois; *Rosa* sp., Mahomet, Illinois; and *R. virginiana*, Fox Ridge State Park, Illinois.

III. Form of *Megastigmus aculeatus* not identified.

(1) Germany. Reported as "*Torymus punctum*," Foerster (1841), and "*Megastigmus flavus*," Foerster (1859); as "*Megastigmus vexillum*," Ratzeburg (1848); Heilbronn, from *Rosa*, sp., Crosby (1913) and Bautzen, Sachsen, from *Rosa* sp., Reinhard (1857); as "*Megastigmus* sp.," which, I suspect, is *M. aculeatus*, Doyer (1926).

(2) France. Mont-de-Marsan, Gascony, as "*Megastigmus cynorrhodi*," from seeds of *Rosa sempervirens*, Perris (1876); Oise, Elbeouf, *M. aculeatus*, "Parasite de *Rhodites spinosissima*, *Spilographa alternata*," Coulon (1931).

(3) Denmark. Copenhagen, "Aus Bromme Plantage," Hoffmeyer (1930).

(4) Austria. Vienna, from *Rosa* spp., Wachtl (1884, 1893).

(5) Sweden. "Habitat in Uplandia," July, August, September, as "*Pteromalus aculeatus*," Swederus (1795); as "*Torymus collaris*," "Habitat in Smolandia, Westrogothia et Scania sat frequens," Boheman (1833); "Hakan Ohlssons, Lundae," from *Rosa* sp., Thomson (1875).

(6) Finland. "N: Tvärminne (Vorentaus), Helsinge," lives in seeds of *Rosa*, Hellén (1934); in seeds of *Rosa*, Kangas (1945).

(7) England. As "*Megastigmus transversus*," "on grass in woods, near London," Walker (1833); "parasite of *Trypeta continua* Meig., a dweller in the berries of the rose," Cameron (1879); Morley (1910); "Europe, Britain," Laidlow (1931).

(8) Italy? As "*M. transversus* Wlk. (= *Torymus punctum* Först)," "nelle larve della *Zonozema alternata* Fall. cire *continua* di Mgn.," Rondani (1872).

(9) Russia. Reared from seeds of *Rosa*, Rodzianko (1908); "Larva destroys the seeds of roses (*Rosa*). Known from middle Europe, Japan, China, North America (introduced) and Kurak district of Russia," Rimsky-Korsakov (1932).

(10) Japan. From *Rosa* sp., Yano and Koyama (1918); in rose seeds, Japan (Anonymous, 1926); Japan and Europe, "parasitic in seeds of rose," Ishii (1932).

(11) China. From rose seeds imported from Peking. Specimens in collection of U.S. National Museum, Crosby (1913).

(12) New York. Ithaca, from *Rosa*, Crosby (1913); Leonard (1926).

(13) Rhode Island. Kingston, from seeds of *Rosa multiflora*. Specimens in collection of U.S. National Museum. Dated June, 1941.

(14) Maryland. Rockville. In house, March, 1944. Specimens in collection of U.S. National Museum.

(15) Washington. Seattle. Specimens in collection of U.S. National Museum. Dated September 31, 1944.

Spread of M. aculeatus. The fact that *M. aculeatus* was originally de-

scribed from Sweden 160 years ago, in 1795, and its wide occurrence from western Asia to England, constitute strong indications that the species is indigenous to the Old World. Its nativity in Eurasia is suggested also by its comparatively recent discovery in Japan, China and North America. The egress of the species from the place of its origin was favored by two conditions. First, it appears to prefer as hosts such roses as *eglantaria* and *canina* of Europe, and *virginiana* of North America, which also are favorites of gardeners, hence are widely distributed through commercial channels. These are the species from which all but a few of my specimens were obtained. Second, the mature larva inhabits the achenes in the hips, undergoing a diapause beginning in midsummer and terminating about April to May of the following year. Since the ripe hips commonly persist on the rose bush until the spring after their development, and the rose hosts, desired for their economic importance, are generally distributed by dealers during the period when the chalcid larva is in diapause, the spread of *aculeatus* is greatly aided by human agencies, both from continent to continent, and from one country to another. On the other hand, the chalcid appears not, or little, to disseminate locally to native roses in Illinois through its own powers of flight.

The major specific means of international spread is through shipment of the "seeds" of *Rosa multiflora* from the orient to Europe and North America. The multiflora rose appears very well adapted to the success of *M. aculeatus*, as is indicated by the large numbers reared from its achenes in Europe (Hoffmeyer, 1929; Doyer, 1926), and in New Jersey (Weiss, 1917). Today, and for some years past, the multiflora is and has been advocated and employed in the United States as an ornamental in parks, as a fence to confine domestic animals, and as a shelter for game animals.

Sex ratio. Whereas *M. nigrovariegatus* involves approximately equal numbers of males and females, *M. aculeatus* produces a strongly disproportionate percentage of females over males, hence is decidedly parthenogenetic. This fact holds for all reports of large numbers reared, as follows: "more than 800 females and 25 males" reared by Hoffmeyer (1929) in Denmark from *R. multiflora* grown in Japan; 1,147 adults reared at Urbana in 1946 to 1953 from *canina*, *eglantaria*, and *virginiana* that originated in New York, North Carolina, Ohio and Illinois totaled 34 males and 1,113 females, a ratio of 1 to 33; two males among "a very large number of females" in France (Perris, 1876); and Reinhard (1857) reared "large numbers" of females, but no males, in Germany. The numbers given by Hoffmeyer (1929) indicate a proportion of the sexes very similar to those quoted above.

Life cycle. The dates of emergence of adult *M. aculeatus* from hips indicate that it completes one cycle in a year in all areas where it has been observed. With few exceptions, the adults are reported to emerge in May and June. Specimens dated decidedly earlier or later than these months were probably either forced in artificial warmth, reared in subnormal temperatures, or discovered as dead some weeks after they issued.

Emergence dates that fall within May and June are as follows: May 2, Kingston, Rhode Island (U.S. National Museum); May 13 to June 24, my lot of 1,147 individuals; June, France (Perris) and Western Russia (Nikol'skaya); May and June, Austria (Wachtl); latter part of May, New Jersey (Weiss); June 26, Finland (Hellén), and May 9 and 25 (Milliron).

Only Reinhard (1857) seems to have seen the females "boring," or ovipositing into the hips of wild rose. The eggs are probably inserted into the immature achenes, where, it may be supposed, the larvae also develop. Oviposition begins a few days after the adults leave the old wintered hips, or approximately from mid-May to July.

Weiss (1917) observed that the "larva appears to destroy the entire interior of the seed, leaving nothing but the hard outer covering." On March 5, 1953, I opened a sample of achenes that had hung during the previous winter on a bush of *Rosa virginiana* in Fox Ridge Park, Illinois, and found full-grown larvae snugly filling the achenes. The emergence of adults from hips of the same source in May and June is evidence that the wintered mature larva pupates in the achenes, probably from late April to June. Reinhard (1857) stated it pupates in the hip, probably a deduction from his observation that the adult, and not another stage, issues from the hip. Wachtl (1884) observed circular holes for escape both in the achenes and in the hypanthium. Accordingly, the larva must develop in the "seeds," not in the fleshy outer cover, nor as a parasite within the larva of *Rhagoletis alternata*, as had theretofore been supposed to be its habit.

The larva grows up as a phytophag, consuming all the seed while this remains more or less soft, and becomes full-grown about midsummer when the seed hardens, undergoes a long diapause and winters as a mature larva in the now seedless achene, pupates in late April to June of the next year, and emerges as adult in May or June.

Economic importance. Commercial damage has been reported where *M. aculeatus* develops in the seeds of the "multiflora rose," *Rosa multiflora*, which is still being advocated and used extensively as a fence to confine farm livestock, as cover for game animals and as a rural ornamental. Weiss (1917) stated that rose growers in New Jersey complained, at different times during the preceding years, of the failure of the seeds

of Japanese *Rosa multiflora* to germinate. Consumption of the seeds by the larvae of *M. aculeatus* was found to be the cause. Weiss reared *aculeatus* from nearly every shipment of seeds consigned from Japan to New Jersey in 1917. An anonymous article from Japan (1926) named *M. aculeatus* in rose seeds as one of the principal pests found in plants intended for export. As an indication of the destructive potential of *aculeatus*, it is also significant that Hoffmeyer (1929) reared more than 800 adults from the seeds of *R. multiflora* shipped from Japan to Denmark. Doyer's (1926) report that a *Megastigmus* sp., which may have been *aculeatus*, was reared from seeds of *R. multiflora* at the seed-testing station at Wageningen, Germany, indicates this is a species capable of large populations in favorable rose hosts.

Megastigmus nigrovariegatus Ashmead, The American Rose Seed Chalcid

Type localities and synonyms. Ashmead's description (1890) of *M. nigrovariegatus* was based on a number of females that were collected at Greeley, Colorado, and Vancouver Island, British Columbia, by H. F. Wickham. The male was described by Crosby (1913) from a series preserved in alcohol, without giving data. Milliron (1949) redescribed this sex from specimens reared from seeds of *Rosa rugosa*. There are no synonyms, except two which resulted when Crosby (1909) confused *nigrovariegatus* Ashm. with *aculeatus* Swed., and Laidlaw (1931) misspelled the specific name as "nigrovarietus." These nomenclatural errors are pointed out by Milliron (1949, p. 295).

Hosts and distribution. Both the rose hosts and geographical sources for *M. nigrovariegatus* are known, as indicated in the following list.

Rosa acicularis vars., Fairbanks, Alaska (U.S. National Museum); seven locations in northwestern Canada to near Fairbanks, Alaska (Balduf, original); Eaglesnest, Ely, Tomahawk road, Temperance river at Lake Superior, in northeastern Minnesota (Balduf, original).

Rosa blanda vars., Eaglesnest, Ely and Grand Marais in northeastern Minnesota; Solon Springs, Gordon and Sarona, Wisconsin; Ottawa, Canada; Atkinson, Illinois (Balduf, original).

Rosa blanda and *R. carolina* vars., Chetek and Rice Lake, Wisconsin (Balduf, original).

Rosa carolina vars., Fall Creek, Endeavor, and Black River Falls, Wisconsin; Ironton, Missouri; the following localities in Illinois—Apple River State Park, Freeport, Kirkland, Rochelle, Wichert, Watseka, San Jose, Mahomet, Mayview, Philo, Urbana, Kickapoo State Park, Ridgefarm, Alton, Velma, Taylorville, Sumner, West Frankfort (Balduf, original); Champaign county (Balduf, 1945).

Rosa rugosa, Madison, Wisconsin (Crosby, 1909, 1913), Dane-Columbia county line on U.S. 45, and Ashland, Wisconsin (Balduf, original); Minneapolis, Minnesota (Milliron, 1949); Urbana and Sidney, Illinois (Balduf, 1945), Onarga and Taylorville, Illinois (Balduf, original); Kingston, Rhode Island (U.S. National Museum); Orono, Maine (Balduf, original).

Rosa palustris, Urbana, Illinois, and Homeworth, Ohio (Balduf, original); Urbana, Illinois (Balduf, 1945); Vienna, Virginia (U.S. National Museum); Virginia (Milliron, 1949).

Rosa eglanteria, Champaign county, Illinois (Balduf, 1945); Kickapoo State Park, Illinois, West Lafayette, Ohio (Balduf, original).

Rosa spinosissima and *R. xanthina*, Urbana, Illinois (Balduf, 1945).

Rosa virginiana, Urbana, Illinois (Balduf, 1945); Orono, Maine (Balduf, original); Vienna, Virginia (U.S. National Museum).

Rosa Macounii, Eaglesnest, Minnesota; Saskatoon, Saskatchewan; Crete, Nebraska (Balduf, original).

Rosa setigera, Urbana, Illinois (Balduf, original).

Rosa arkansana, Poynette and Madison, Wisconsin (Balduf, original).

Rosa woodsii, Beulah, Manitoba, and Provo, Utah (Balduf, original).

Rosa californica, Albany, California (Balduf, original).

Rosa pyrifera and *R. lunelli*, Saskatoon, Saskatchewan (Balduf, original).

Rosa spaldingii, Pullman and Spokane, Washington (Balduf, original).

Rosa ultramontana, Moscow Mts., Idaho (Balduf, original).

Rosa suffulta, Saskatoon, Saskatchewan; La Harte, Illinois (Balduf, original).

Adults of *M. nigrovariegatus* have also been reared from hips of undetermined wild roses sent to me at Urbana by collaborators from West Alexandria, Ohio, 1947; East Falls Church, Virginia, 1946; and from samples of hips sent in 1953 from the following places in Iowa; state park at Keosauqua; "Strawberry Point"; Black Hawk State Park; Lakeview; Waubonsi State Park, Hamburg; Lake Aquabie State Park, Indianola; Oak Grove State Park, Hawarden; Chariton, and Beeds Lake State Park, Hampton. I also have this species from hips taken at Kenosha Pass, Colorado.

Crosby (1913) had *M. nigrovariegatus* "from seeds of roses" obtained in New York, Illinois, New Hampshire, Massachusetts, Delaware and Utah. According to data on specimens in the collection of the U.S. National Museum, the chalcid occurs in Canada, Illinois, Washington, D.C., Maine, Idaho, Colorado, British Columbia, New York, Pennsylvania, Massachusetts, Virginia, Minneapolis and Alaska. Cockerell (1894, 1899) found it on a rose at Santa Fe, New Mexico, and Britton (1938) reported it for Connecticut. Milliron (1949) adds the following provinces

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or states: Nova Scotia, Quebec, West Virginia, Indiana, Michigan, Kansas, North Dakota, and Oregon.

Our first indication of the host plant of *M. nigrovariegatus* came from the observation of Cockerell (1894), who discovered females "on the fruits of roses in Mr. Boyle's garden" in Santa Fe, New Mexico. Cockerell considered it "extremely probable that the species breeds in rose fruits." Crosby (1909) observed females ovipositing on the rose hips during June and July, at Ithaca, New York, and his discovery of larvae and pupae in the seeds of rose established that rose seeds are their specific niche and food, a fact which is now generally accepted. In view of this knowledge, earlier claims that *M. nigrovariegatus* is an entomophagous parasite are untenable.

Milliron (1949, p. 297) relates two such instances of error, both originating from data on old specimens in the collection of the U.S. National Museum. In one of these cases, originally published by Crosby (1913), the alleged host was a moth, "*Clisiocampa plumalis*," under observation at the Washington Agricultural Experiment Station in 1898. This record was subsequently copied by Maria Rühl (1914).

In the second instance (Riley, 1893), the host was said to be a gall-forming cynipid, "*Callirhytis scitulus* Bassett." Two of the three specimens, to which Riley referred, were rediscovered and examined by Milliron (1949), who found they were "small atypical *nigrovariegatus*" and commented that "their identity throws all doubt on the correctness of Riley's note." It is of interest also that Riley (1893) had cited this case in support of his contention that *Megastigmus*, as a group, is essentially parasitic, chiefly on gall-making Cynipidae.

Summary of distribution. Of the northerly areas of North America, all excepting Vermont, South Dakota, Wyoming, and Alberta are included in the above list. Probably the chalcid also occurs in these excepted states and provinces. *M. nigrovariegatus* is, accordingly, widely distributed in the northern reaches of this continent from coast to coast. The northernmost recorded occurrence is in the vicinity of Fairbanks, Alaska, at 65° north latitude, and its southern limits lie near the 36th line of latitude, as indicated by the records from New Mexico, Arizona, and Virginia.

Variation (Fig. 52). As stated above, this species is usually readily distinguishable from its much more color-stable relative, *M. aculeatus*. While studying more than 8,000 reared *nigrovariegatus*, I observed that the males vary from entirely yellow on small, to wholly black on large, specimens, with many intergrades in size and color pattern. The variation in color is decidedly less extensive in the females (Balduf, 1957a). More specifically, the females of the present species have ovipositor and sheaths shorter than the body and both sexes have the stigmal knob

surrounded by a narrow, yet distinct fuscous ring. *M. aculeatus* lacks this ring around the knob, and the female bears sheaths and terebra longer than the body.

Concurrence of M. nigrovariegatus and M. aculeatus. Only three of the many lots of hips that I had under observation from 1943 to 1953 yielded adults of both these rose seed chalcids. The essential data pertaining to these three cases are presented in Table 3.

TABLE 3. CONCURRENCE OF THE ROSE SEED CHALCIDS

Sources of hips	Rosa spp.	<i>M. nigrovariegatus</i>		<i>M. aculeatus</i>	
		♀	♂	♀	♂
West Lafayette, O.	<i>eglanteria</i>	0	2	28	0
Kickapoo Park, Ill	<i>eglanteria</i>	0	3	21	0
Fox Ridge State Park, Ill.	<i>virginiana</i>	0	5	65	2

Emergence. Still in the achene in the hip, the newly formed adult discards the pupal theca, then employs the mandibles to cut a circular hole through the pericarp of the achene and the more or less dry hypanthium directly above it. The exits are gnawed through the broadly convex surface of the achene that lies in contact with the concave inner face of the hypanthium. And because the inhabited achenes normally lie in the petiolar area of the hip cavity, the exits are confined to this portion of the hypanthium.

However, the adults do not always succeed in emerging. Dissections of the relatively small achenes on a shaded stand of *Rosa carolina* at Urbana revealed some adults dead in the achenes and still encased in the pupal thecae, while others remained stuck in the partly prepared exits in the achenes. Such fatalities are believed to result from the inadequacy of the small seeds of this rose bush for the development of vigorous larvae. Even the adults that did emerge averaged small for the species (Balduf, 1945).

While rearing adults from hips in the laboratory, Milliron (1949) observed that they usually remained relatively inactive for a day or more after they emerged from the pupal thecae, requiring some time for drying or hardening the wings, or to remove any adhering parts of the thecae before they became very active and engaged in flight.

Sex ratio and protandry. The number of males in relation to the number of females is approximately equal, according to samples reared from hips. Milliron (1949) reports having reared 5,785 adults from a single lot of the hips of *Rosa rugosa* at St. Paul, Minnesota. Of this number,

3,099, or 53.4 per cent were males, and 2,697 were females, or 46.6 per cent. These figures give a ratio of 1.0 female to 1.15 males.

In the years 1943 to 1953, I reared approximately 9,935 adults. These emerged from hips of many species of *Rosa* grown at places so widely separated as Alaska, California, Minnesota, Maine (Orono), and central Illinois. The sample consisted of almost equal numbers of males and females; 5,146 males or 52 per cent, and 4,779 females, or 48 per cent.

My observation (1945) that *M. nigrovariegatus* is definitely protandrous has been confirmed by Milliron (1949). He reported that "in general, males make their appearance about three days in advance of females, and reach their maximum emergence a few days after the latter have begun to emerge. In more restricted numbers they continue to appear along with females throughout the period of emergence."

Some of my data on this feature appeared in my article of 1945, and others were accumulated in subsequent years. On June 3 and the early afternoon of June 4, 1943, only males were present on bushes of *Rosa rugosa* at Urbana. The first females were discovered at 6:00 P.M. of June 4. Males still predominated on June 5, but on June 9, the ratio of females to males was 15 to 1, and on June 13, it had increased 35 to 1. From June 15 to 19, no males remained, whereas 82, 60, 62, 50 and 38 females were present, respectively, on the same five days.

Two other sets of data indicate the nature of protandry in this rose seed chalcid. The first set concerns adults from hips of *Rosa rugosa* stored in large glass tubes through a period of eight successive days. Emergence per day, by sexes, was as follows: first day, 26 ♂s, 3 ♀s; second day, 23 ♂s, 7 ♀s; third, 20 ♂s, 10 ♀s; fourth, 13 ♂s, 26 ♀s; fifth, 6 ♂s, 28 ♀s; sixth, 2 ♂s, 10 ♀s; seventh, 3 ♂s, 0 ♀, and eighth day, 1 ♂, 0 ♀.

The second set of data pertains to 227 females and 135 males reared from hips of *rugosa* between May 22 and June 27. The first males emerged on May 22, the first females on May 25. The numerical peak of emergence of the males was reached in May 26 to 30, that of the females in May 29 to June 4. Both sexes continued to appear thereafter, but the daily issue of females gradually overtook that of the males as the period of emergence progressed, thus repeating the same pattern of relative emergence of sexes demonstrated in the preceding instances and as expressed in the statement quoted above from Milliron.

Similar patterns of protandry were discovered also in other hip insects that develop equal numbers of males and females and were reared in adequate quantity.

Mating. In May and June of the years 1943 and 1944, I observed a strong tendency of adult males to gather on and about certain old hips of *Rosa rugosa* at Urbana, while, at the same time, they avoided many

other hips of similar appearance and age. Then on May 30, 1944, as I stood watching the movements of such an aggregation of males, I discovered the significance of this behavior. Presently the head of a female slowly emerged into view in the corky hypanthium of the hip. No sooner had she completed her emergence than the group of males rushed upon her, and one succeeded in mating. Somehow, they are obviously capable of sensing the presence of adults of their kind still invisible in the hip. It is desirable to learn whether they respond in this manner to emerging males as well as females, i.e., whether they can also distinguish between the sexes while these are still out of sight in the hip.

While thus attracted to the old hip, the males (as many as fifteen in one instance) either rested quietly on it, or on branches and leaves nearby, or sometimes ran excitedly over it, or made short quick flights within a foot from the hip, but always returned again to it. Often some of them vigorously pursued others as if to drive them away. In doing so, they sometimes raised and lowered their wings as resting butterflies may do. Dissections of several hips, around which males had previously concentrated, showed that they no longer contained adults when the interest of the males in the hips had ceased. I believe this is the normal place and time of mating in the field, but have seen a few instances of mating elsewhere than on old hips.

Milliron (1949, p. 384) stated that mating occurs very commonly in captivity and "usually within a few hours after the females emerge from the seeds. However, in a limited confinement with a relatively large population of males aged several days, copulation may occur within the short period of 15 or 20 minutes after emergence of the female."

In Milliron's description of mating activity, I recognize four somewhat distinct steps. First, in approaching the female, the male momentarily examines her with his antennae, becomes much excited and immediately takes a mounted position. Second, during the courting phase, the antennae of the male are vibrated rapidly in close proximity to, or touching those of the female; characteristically he also momentarily elevates the vibrating wings to a vertical position, during which he usually surges somewhat downward and forward, often thereby touching her antennae or head with his mandibles. The wings may be elevated in that way several times before copulation is attempted. Also, if the female is especially inclined to move actively about, the male may drop his wings forward at her sides and hold them there momentarily each time. Third, when ready to copulate, the female slowly elevates the abdomen and lowers the sterna, thereby exposing the genital opening. Instantly the male is in place, and may then copulate from one of two positions, either almost caudolateral—or a directly caudal one. Small males usually did so from the caudolateral position. In either case, the

male quickly moves backward, bends the abdomen into a ventral position, and clings to the wings, the side or to the ovipositor of the mate. Copulation usually requires between 15 to 20 seconds, during which time the female remains in a stationary position with the abdomen elevated. Fourth, after copulating, the male immediately remounts directly from the position taken when *in copulo*, and proceeds to repeat his courting behavior, but in no instance did Milliron observe a second consecutive copulation. Eventually, the male is dislodged by the female, or he leaves of his own accord.

Milliron reported also that large males are usually not successful in mating with small females, but that small males commonly mated with large females. His observation, that small light-colored females from achenes of *Rosa palustris* mated with small males from *R. rugosa*, is fundamental in demonstrating that forms of *nigrovariegatus* from different species of roses can be cross-mated and therefore are not host specific.

As a rule, females mate more than once, according to Milliron (1949, p. 384). My observations pertain to the chalcid on *Rosa virginiana* and other host roses, and have inclined me to the view that repetitions are not likely to occur often because the males seem to restrict themselves to old hips so long as females remain in them, and the newly emerged, mated females soon leave the site of their origin in favor of new hips of the year. While males intermingle with the ovipositing females early in the adult period of the species, they soon become the numerically minor sex, and later are wholly absent while numbers of ovipositing females remain. This probably signifies that the males become widely dispersed, or, rather, that they live a relatively short time. Being a protandrous species, the males do not live so far into the season as the females, even if it be assumed that their lifetimes are as long as those of the females. Matings at the sites of oviposition appeared to be of relatively infrequent occurrence.

Oviposition. The age at which females commence to deposit eggs into the new growing hips has not been satisfactorily determined. That newly emerged individuals do not contain eggs ready for deposition was demonstrated by Milliron, who examined the ovaries. My observations in 1944, indicated that the first eggs are laid when the females are about five days old. According to Milliron (1949, p. 385), females that are prepared to begin ovipositing, frequent more consistently the ends of the branches where hips are borne. At this time, many hips are "still green and contain soft seeds in which the cotyledons are small and enveloped in a watery or jelly-like medium. Ordinarily rose hips such as these constitute the type in which early egg depositions are made, but as the season progresses, somewhat older fruits must be selected. Rose hips are entirely unsuitable for oviposition after they become red and

contain seeds with hard coats and firm cotyledons." I have observed (1945, p. 193) that "oviposition is in progress when the hypanthium and pericarps are still soft and the seeds remain in a semiliquid pulpy state." The period of time during which seeds exist in this favorable condition for oviposition is prolonged by the development of several "sets" of hips in chronological succession.

The following description of procedure in oviposition represents an integration of observations from the accounts published by Milliron (1949) and myself (1945). Employing her antennae, the female may carefully examine the entire surface of the hip before a location on it is finally selected. This place is necessarily restricted to the basal portion of the hip where the developing achenes lie. There the female stands with legs widespread to hold her to the hip surface. Wavering movements of the body begin as soon as the location is selected. The abdomen is next elevated sharply and strongly arched, and the caudal end brought forward ventrad. Thereby the long sheath and the contained ovipositor, or terebra, are moved ventrocephalad from their usual dorsocaudal resting position until they stand perpendicular to the hip and their tips contact its surface. Next, the sheath is released, presumably when the terebra has superficially pierced the hypanthium, and flips backward, at first assuming a horizontal posture, then gradually a vertical position as the terebra penetrates deeply into the hip. The sheaths are more rigid than the terebra itself, and therefore are a means of bringing this drill into the required position and also appear to assist in the initiation of drilling by preventing it from bending as pressure is applied on it from the abdomen. During the short time required to insert the terebra, the antennae are held porrect, the wings in an inclined position, and the thorax, and especially the abdomen, waver slowly and conspicuously. The ovipositor does not always enter the hypanthium in a steady continuous manner, but drills by a series of alternating thrusts and partial withdrawals. When the terebra is entirely inserted, the abdomen becomes more natural in shape; its venter then almost or actually contacts the surface of the hip. A brief interval of inactivity follows the insertion of the ovipositor during which the egg is presumed to pass from the oviduct into the seed. The terebra is then withdrawn in a quick steady manner and at once snaps back into the sheath; these structures then resume the original resting posture. The female then may turn about to examine the puncture, but as often directly seeks another location to repeat the oviposition. In several instances observed in 1943 and 1944 at Urbana, particularly on *Rosa virginiana*, females appeared unable to withdraw the terebra from the hip, and were found dead suspended by that appendage.

The time required for each of several ovipositions was between 4 and

7 minutes, although some required as much as 15 minutes (Milliron). In a number of depositions observed on *Rosa rugosa* at Urbana, the whole process consumed from 100 seconds to 10 minutes. Milliron found that unsuccessful attempts to insert eggs are characteristically of shorter duration.

Milliron (1949, p. 386) related that individual females which have deposited several eggs in a hip may become thoroughly accustomed to that hip and take possession of it, behaving in a manner as if to guard against oviposition by others. They move about excitedly with the wings elevated or inclined, and make thorough examinations of the hip at varying intervals, driving away any intruding females. Occasionally the intruder refuses to depart and a furious battle ensues in which the invading female may be the victor and herself take possession.

The time of day when oviposition is performed is evidently determined by the prevailing temperatures. Concerning this point, Milliron (1949) stated that "on warm days, oviposition is seldom noted in the direct rays of the sun during hours with maximum temperature," but it "is continued in the shade during this time. Females restrict much of their oviposition on such days to the early morning or late afternoon hours." The same relation between oviposition and temperature was observed at Urbana (Balduf, 1945). On June 17, 1943, 60 females were visible in the morning when the *rugosa* rose was shaded by trees and buildings; only 43 were exposed in the warmth of the early afternoon; 63 females came into view when evening shades again cooled the rose bush. Likewise, the thrice daily counts were 50, 20, and 41 on June 18, and 18, 5, and 13, respectively on June 20. In the mornings and evenings, the females moved about in full view on the new hips or leaves, and a number engaged in oviposition, whereas in midday they resorted to the shelter of leaves, and laid eggs only in hips that were then shaded. On the above dates, midday temperatures rose to 90 degrees or above in the sun.

Egg and embryo. I found eggs and small first instars lodged in the soft tests of the seed or in the end of the seed that lay nearest the hypanthium. Milliron (1949, p. 374) observed that "eggs are deposited entirely within the jelly-like mass surrounding the seed embryo, and the end of the anterior pedicel is attached usually to the side of the innermost envelop of the endosperm."

The terebra appeared usually to bore only through the hypanthium of the hip and into the cortex of the achene to place the egg into the seed substance, and infrequently deeper than the outer layer of achenes into the secondary underlying tier. Obviously, the depth to which eggs are placed may be determined by the relative length of the terebra and the thickness of the hypanthium, if not by the texture of the achene and

seed coat. Approximately 95 per cent of the larvae of *nigrovariegatus* which I dissected from achenes of *Rosa rugosa* in 1943-44 (1945) occurred in the outermost layer of fruits, the rest in the next deeper layer.

We are indebted to Milliron (1949) for much of our knowledge of the embryonic, larval, and pupal stages of *M. nigrovariegatus*. These stages are illustrated in his Figures 32 to 44.

He has described the egg as comprising a long, narrow anterior pedicel, an elongated oval body, and a short, spurlike posterior pedicel. Ovarian eggs measured an average of 0.985 mm. They are grayish white, turgid, and the surface smooth, shining and without ornamentation. The average length of eggs measured after deposition was 1.477 mm. The posterior end of the deposited egg usually becomes slightly attenuated, and the entire egg is somewhat more elongated. The anterior pedicel finally collapses to a ribbon-like form except sometimes its distal part. The posterior pedicel, which is sometimes wanting, is either extended, recurved toward the body of the egg, or appressed to its surface. The ovaries are "meroistic-polytrophic."

Dissections of several gravid females revealed the presence of 10 to 25 fully developed eggs per individual. These numbers do not represent the reproductive capacity of single females. In all late embryos examined by Milliron, the cephalic end was directed toward the end bearing the long, narrow pedicel which later collapses into a ribbon form. Prior to hatching, the embryo becomes separated from the chorion and surrounded by a colorless fluid. Shortly before eclosion occurs, a delicate longitudinal trachea can be seen in each lateral region of specimens placed in glycerine. By their outward movement, the conspicuous mandibles of the late embryo appear to rupture the chorion and effect eclosion.

Larval life. According to the studies by Milliron (1949, p. 376), the developing larva of *nigrovariegatus* comprises five instars. He ascertained this "originally by size, shape and degree of sclerotization of the mandibles, and by the presence of setae on the body segments. In order to check the instars as discovered by using these characters," he made a limited number of measurements of the widths of the head, and these likewise indicate that five instars do occur. The size of the head capsule appears to be very significant as an aid in recognizing the second, third and fourth instars, which usually offer much difficulty. The larger setae present on the fifth instar readily distinguish it from the fourth. The instars are described fully by Milliron (1949, pp. 377-79, and his Plate 5).

Because it is an excellent statement of original observations on larval development in the seeds, I quote Milliron's account in full: "It has been pointed out that more than one egg may be placed within a single

seed. If such be the case and the resulting larvae do not come in direct contact with each other, they may continue to develop through approximately the third instar. Increase in size of the seed embryo, as well as increase in size of the larvae themselves eventually force them into contact with each other and cannibalism results. Frequently two or three larvae, representing as many instars, are found in a single seed but in no instance does more than one complete its larval development. The occurrence of more than one young larva per seed is especially common during the early part of the oviposition period. During this time, when the seed embryo is yet comparatively small, the greater part of the seed content is watery to jelly-like in consistency, and the young larvae may be located almost anywhere inside consuming this material without any apparent damage to the seed or without impairing its growth. As the seed embryo grows, the surrounding medium becomes grayish white and paste-like, and at or during this stage a larva is commonly forced to the distal end of the seed or it may come to lie to the side of one of the cotyledons. In either event, when the larva is ready to begin feeding on the cotyledons, there is every assurance that it will not begin at the base of the seed embryo, which continues to enlarge and provide ample food for the larva to complete its development. The outer covering of the endosperm mostly remains intact until the later larval stages are attained when it is then consumed along with the basal portion of the embryo."

I have observed that the larva consumed all of the seeds excepting small hard dry brownish particles which remain scattered throughout the seed cavity and over the full-grown body. Probably incidental to its writhing movements, the full-fed larva works this frass to the narrower anterior and posterior ends of the seed cavity where it becomes compacted into two concave caps, shaped to the ends of the body and the cavity.

The distinction between full-fed or full-grown larvae and mature larvae warrants a note. The alimentary tract of full-grown individuals is distended with a mixture of dark reddish to purple food and fecal waste, that gives the larva a dark color and fills the seed cavity of the achene so snugly that removal of the larva without puncturing the body wall requires great care. Some weeks after the larva has become full-fed, it has attained maturity, having utilized, physiologically, a considerable part of the colored stuff in the tract so that the body is now noticeably paler and shrunken and fills the cavity loosely. By April, i.e., after hibernation and shortly before pupation, only a small cluster of black solidifying pellets of feces remain to darken the midabdominal area of the matured body.

Transformation. The process of change from larva, through prepupa,

to pupa have been described by Milliron. The larvae which are about to become prepupae are sluggish, somewhat contracted, and expel black pellets of excreta. The abdominal region becomes somewhat arched and distinctly differentiated from the thorax as the external form of the pupa within is developing. Conspicuous imaginal buds on the lateral and lateroventral surfaces of the thorax mark the approximate locations of the wing pads and legs of the future pupa. The pupal head can be seen within the prothorax. The completed prepupa has a form intermediate between larva and pupa.

At the end of this stage, the larval cuticle becomes slightly flaccid. The initial break appears on the thorax, and seems to be caused by pressure applied there by the contractions of the pupal abdomen within. The cuticle is slowly forced backward, chiefly by the contractions and expansions of the abdomen. When the prepupa was removed from the normal situation in the seeds, this process required one or two hours.

The changes in color undergone by the pupa from its beginning were described by Milliron (1949, pp. 381-82). The body of a pupa that is about to molt and disclose the adult, is no longer turgid; the theca loses its gloss and smoothness, and becomes greasy in appearance. The pupal theca is broken across the pronotum or just behind the head; the break results from increase in activity of the body and legs, and contractions of the abdomen that appear to concentrate pressure on the cephalic end. By its expansions, contractions and bending, the abdomen plays a most significant role in effecting the molt, although once the theca passes back to the abdomen, the hind legs may also be employed in removing it. Once exposed, the wings expand as a consequence of fluid forced into them from the body cavity, and this pressure also appears to be the principal means of removing the theca from the wings. That part of the theca still intact on the head and antennae is discarded with the aid of the front legs.

Life cycle. Crosby (1909) has given data relative to the chronological distribution of the main events in the life cycle of *nigrovariegatus*. These show that it completes one generation in a year at Ithaca, New York. He observed that the adults emerge through round holes from the "seeds" in the hips, and may be found ovipositing on the rose hips during June and July. The larvae, according to Crosby, become full-grown in the fall, when they so nearly fill the seeds that it is very difficult to remove one without crushing it. These mature larvae pass the winter, then pupate the next spring. Balduf (1945) and Milliron (1949) have published additional data, which essentially confirm while supplementing the facts from Crosby (1909). Since 1945, I have gathered many additional records relative to the dates of emergence of adults and host

relations from hips obtained in Illinois and other states. The data presented from Milliron pertain to St. Paul, Minnesota.

In the years 1947 to 1951, I reared approximately 4,200 adults at Urbana, from hips of several *Rosa* spp. obtained from Alaska, northeastern Minnesota, Wisconsin, Saskatchewan and east central Illinois. In the over-all period, adults issued between May 12 and July 31, or 81 days. The yearly periods were, of course, considerably shorter, i.e., 51, 47, 57, 52 and 36 days, respectively. In 1943 and 1944, the first adults emerged from *R. rugosa* on June 3 and May 25 (Balduf, 1945). Unpublished records from the files of the University of Minnesota are cited by Milliron (1949): in 1914, emergence began at St. Paul about June 4, largest numbers emerged on June 15 and 23, and high numbers appeared consistently between June 22 and 26, after which, numbers per day decreased gradually to July 7; in 1939 and 1940, Milliron noted the largest population and maximum activity during the second and third weeks of June. Hips of *R. rugosa* taken by me at Ashland in northern Wisconsin and transported at once to Eaglesnest, Minnesota, yielded their seed chalcids between July 2 and 29, 1945. A quantity of hips of *R. acicularis* picked at Eaglesnest and also wintered there, yielded the chalcids between late June and July 6, 1949.

These cases involving Ashland and Eaglesnest reflect the retarding influence of the cooler northern spring climate. On the other hand, lots of hips native to Illinois yielded the seed chalcids 3 to 16 days later than did lots of hips native to Maine, Minnesota, Wisconsin, the Rocky Mountains and Alaska, but wintered at Urbana. This may mean that the chalcids acquire some tolerance for the more stringent northern climate in which the larvae matured, and that this tolerance was not wholly lost in the interval spent in the moderate climate of central Illinois.

Milliron (1949, p. 389) made laboratory tests to determine the survivability of this seed chalcid under varied conditions of temperature and humidity. In all cases cited here, the temperature was held at 15° C., the food consisted of soaked raisins and, later, solutions of brown sugar, and the samples involved 101 to 314 individuals, except one of 17 females. When the relative humidity was held constant at 30 per cent, males lived an average of 18.83 days, and the sample of 17 females averaged 21.24 days. Under identical conditions, but with humidity inconstant, the average survival of males was 36.45; of females, 49.62 days. In another test, the moisture was not regulated, and no food or water were supplied. Males averaged 5.06; females, 7.65 days.

From those experimental data, males may be estimated to live three or four weeks in nature, and females a somewhat longer time. If so, the chalcids may be expected to occur in nature at Urbana from late May

to the first part of August. I have seen females as late as July 30 (1947) at Urbana.

According to Milliron (1949, p. 375), the incubation period of *M. nigrovariegatus* is "relatively short and probably does not exceed four or five days." At Urbana, the over-all embryonic period, or "egg stage," extends from late May to early July. I saw females ovipositing as early as June 3, 1944, and June 4, 1943, and as late as July 30, 1947, which indicates that some embryos may be found early in August if suitable rose hips for reception of the egg are then present. However, females are usually few by late June, hence the peak of the embryonic period occurs through the month of June.

The earliest possible oviposition could not have been much before mid-June, 1939, at St. Paul (Milliron). Almost identical results are cited for 1940. Because the season of 1941 was two weeks earlier, Milliron believed oviposition could not have begun before the first week of June. The peak of oviposition appeared to be during the third week of June, 1939, and the activity had ceased by July 10. In 1940, females were seen ovipositing until the middle of July, but in 1941 the peak was reached by mid-June; none were found ovipositing between July 3 and 11.

At Eaglesnest, I saw females oviposit on wild roses from July 15 to 26, 1945, and on July 15, 1950. Since these were but casual observations, it is reasonable to assume that the species probably oviposits there both before and after the dates given.

Because the period of embryogenesis is probably only four or five days long, the inception of larval life is almost simultaneous with that of oviposition. Milliron (p. 376) learned from dissections of inhabited achenes that growth of the larva through all its instars is completed in a month or less. Full-grown larvae were commonly obtained by July 19, in 1939, and by almost the same date in 1940. He discovered numerous submature larvae in achenes on June 30, 1941. In Urbana, at intervals of time, I dissected samples of achenes which showed that the over-all development of the larvae from hatching to maturity, or near it, took place from mid-June to late July, 1943, and 1944.

However, the larval period does not terminate when the larva reaches its full-fed, full-grown state through late June and the first two-thirds of July. With few exceptions, the species persists, without perceptible change, as a full-grown larva through the remainder of the summer, the fall and winter, and to about April 20 to early June of the next year. Since this diapause is initiated in the warmest season of the year, it apparently may not be attributed to low temperatures, but probably to some nutritional or chemical factor in the seed substance ingested by the later larval instars.

The full-grown, mature larval state usually terminates with transformation to the pupal form in the spring following the year of larval development. For exceptions, see "Precocious pupae," below. At St. Paul, this transformation occurred "during the latter part of April or the early part of May," according to Milliron (1949). He found also that the prepupal period averages about three days in length under laboratory conditions. The pupal stage of females varied from thirteen to sixteen days, and that of the males was about twelve days. "Under conditions of cooler outside temperature, this period is probably considerably longer. On the other hand, full-grown larvae retarded until July, when both outside and inside temperatures were approximately the same, passed through the pupal stage as follows: female, twelve days; male, eight days."

Achenes dissected at Urbana at intervals during April and May showed that pupation began during the last ten days of April, 1943, and 1944; also that the peak of pupation was reached between May 8 and 22, and pupal life terminated with emergence of the adult from mid-May to June 20 of these years.

Precocious pupae. While dissecting achenes of *Rosa rugosa* at Urbana, I discovered five pupae of *M. nigrovariegatus* in decidedly unusual seasons of the year, one on November 28, 1942, and one each on July 16, 21, 28, and 29, 1944, respectively. Instead of delaying pupation until the following spring, as is usual for the species, these had transformed to pupae in the same year in which the larvae developed. One of the pupae of 1944 was still white when found, but the rest had advanced to the brown color phase, which suggested that they would soon have become adults. Both sexes were represented, and all were large and vigorous in appearance, reflecting the favorable volume of the seed contained in the achenes of this rose. These physical features of the seed may afford clues to the cause of the premature pupation observed here.

An alternate possibility as to the cause of the precocious pupation is suggested by the work of Williams (1958) on the juvenile hormone in certain macromoths, and the observations by Milliron (1949) on cannibalism in this rose seed chalcid. In his studies Williams implanted the corpora allata of the young larva of *Bombyx mori* Linn. into the fifth instar, and found the latter continued to grow and then changed into a giant pupa and adult. Milliron observed that cannibalism among the larvae of *Megastigmus nigrovariegatus* is common in the achenes of *Rosa rugosa*, and eventually only one individual survives. These facts from Milliron and Williams served to suggest that larger larvae of the seed chalcid, when consuming smaller ones in the achene incidentally obtain an increased supply of juvenile hormone that may influence the development of larger-than-normal larvae, followed by precocious pupa-

tion, quite apart from the food supply, indicated above as the cause of precocity.

Acceleration of the life cycle. Although the single annual cycle is normal for *M. nigrovariegatus*, its duration may be greatly shortened by subjecting achenes inhabited by the mature larvae to unnatural treatment. This fact was established experimentally by Milliron (1949, p. 383). In late summer, the environmental temperature of such achenes was gradually lowered to zero centigrade, or slightly below, and held for approximately a month, and then gradually returned to room temperature. A few adult males emerged from these achenes during the middle of October. The larval diapause was shortened by about six months.

PARASITES OF *Megastigmus nigrovariegatus*

Eupelmus, Eupelmidae, Hymenoptera

In the spring of 1944, I found a few dead, dry greenish chalcids in the achenes of *R. rugosa* at Urbana. Dr. B. D. Burks identified them as a species of *Eupelmus*. The circumstances of their occurrence indicated they were parasites of *M. nigrovariegatus*.

In subsequent years, I obtained 25 living adults of an *Eupelmus* sp. from jars containing rose hips acquired as follows: Taylorville, Illinois, one male, May 27, 1947, from old hips of *Rosa canina*; San Jose, Illinois, one male, August 16, 1951, from live hips of *R. carolina* picked July 21, 1951; Eaglesnest, Minnesota, two females, September 18 and 21, 1951, from new hips of *R. acicularis*; Chetek, Wisconsin, one male and twenty females, September 9 to 30, 1948, 1950, and 1951, from hips of *R. blanda* and *carolina*.

It is now not known whether one or more species are represented in this series of 25 adults, nor has it been established what the hosts may be. It is possible this is the same species found dead in the achenes of *rugosa*, as stated above. Again, it may be the species whose first instar I discovered in the larva of *Rhagoletis basiola* (see p. 50). Evidence from the host relations of *Eupelmus* spp. recorded in the literature (Muesebeck, et al., 1951), would indicate that it may attack directly either *Rhynchites bicolor* or *Cydia packardi*, or some of the primary parasites of these phytophags in rose hips.

ADDITIONAL PARASITIC HYMENOPTERA FROM HIP JARS

Ten species of parasitic Hymenoptera have been obtained in addition to those previously described in connection with their hosts. These orig-

inated in jars containing hips of several species and localities. All are represented by one to several specimens. I have no certain information about their host relations. Below is given a list of the species merely for the sake of whatever interest they may prove to be in the future.

Trimorus columbianus (Ashm.), Scelionidae, Proctotrupoidea.

Haltichella sp., Eupelmidae, Chalcidoidea.

Eupelmella vesicularis (Retz.), Eupelmidae, Chalcidoidea.

Tetrastichus faustus Burks, Tetrastichidae, Chalcidoidea.

Zatropis incertus (Ashm.), Pteromalidae, Chalcidoidea.

Sympiesis aencylae Gir., Eulophidae, Chalcidoidea.

Campoplex sp., Ichneumonidae, Ichneumonoidea.

Pycnocryptus director (Thbg.), Ichneumonidae, Ichneumonoidea.

Cymodusa distincta (Cr.), Ichneumonidae, Ichneumonoidea.

Orthopelma mediator (Thbg.), Ichneumonidae, Ichneumonoidea.

SUMMARY

Thirty species of animals are now known to comprise a microcommunity which centers in the rose hip. With the exception of the mite, *Caloglyphus*, and the annelid worm, *Chaetogaster*, all the members of the community are holometabolous insects. Their larvae develop either in the hypanthium or the achene cavity of the hip, hence are obligatory, while the embryo, pupa and adult sustain no single positional relation to the hip. The hexapodous adherents to the community constitute three distinct bionomic groups, or strata, when classified with reference to food preferences and the niches they occupy. First, are the phytophags which feed directly upon the living substance of the hip; second, the predatory and parasitic members, which attack some stage or stages of the phytophags, and third, species of scavengers that feed upon the waste materials that result from the first and second groups. The bionomic features of these several groups are summarized below in the sequence in which they are described in the foregoing pages.

The phytophagous species are members of four major orders of insects, Diptera, Lepidoptera, Coleoptera and Hymenoptera. The Diptera are represented by three species of Tryptidae—*Carpomyia Schineri* and *Rhagoletis alternata* of Europe, and *Rhag. basiola*, widely distributed in northern North America. *Rhag. basiola* places the eggs singly in pits bored into the hypanthium, the larva feeds on the fleshy tissue here and, when mature, emerges and pupariates, presumably amid duff on the ground. Development then advances to the early phase of the pupa, in which stage the species winters. Pupation is resumed in May and

June of the next spring, and flies appear as the new crop of hips develops during the summer.

The observations made in Europe on *Rhag. alternata* and *Carpomyia Schineri* strongly indicate that their relation to the hips and the seasonal distribution of the life stages are very similar to those of *Rhag. basiola*.

Rhag. basiola is attacked by four species of solitary endoparasitic Hymenoptera—two Braconidae, *Opius baldufi* and *O. rosicola*; a pteromalid chalcidoid, *Halticoptera rosae*, and a species that appears to be a eupelmid chalcidoid. The species of *Opius* place eggs into the instars of *Rhag. basiola*, the larva persisting as a first instar until the host larva matures, leaves the hip and pupariates. The parasite then molts and quickly completes its larval growth in the puparium, consuming the host before it can pupate, and passes the winter as a mature larva in the puparium. Pupation and emergence of the adult occur in May to July after the hibernating period.

In contrast with *Opius*, *Halticoptera rosae* inserts the egg into the egg of *Rhag. basiola* in the hypanthium. Its larval life begins in the host embryo, and continues as a first instar while the host undergoes its three larval stages and winters as an early phase pupa. The first molt apparently occurs when the host resumes pupation the next spring. In a few days, the parasite completes its growth, destroying the host pupa. *H. rosae* pupates in the puparium of *Rhag. basiola*, and the emergence of the adult in June and July antedates that of the *Opius* species.

Only the first instar of the eupelmid species was seen. It occurred both in the larval stages and the puparia of *Rhag. basiola*, and hence may undergo a prolonged diapause in the first instar, as *H. rosae* does.

The moths, *Carposina scirhosella*, Carposinidae, and *Cydia roseticolana*, Olethreutidae, are native to Europe, whereas *Cydia packardi* is American. The female *packardi* cements the eggs mostly to the "neck" of rose buds and rose hips. There is one generation yearly in northeastern Minnesota but two in east central Illinois, the first developing largely in buds, the second in hips. The caterpillar feeds within the rose bud and in the hypanthium of the hip, and, when mature, emerges to spin up in various places of concealment. The winter is passed as a mature larva, and pupation takes place in April and May.

The observations made on *Cydia roseticolana* and *Carposina scirhosella* in Europe indicate that their cyclic development and relation to the hip are very similar to those of *Cydia packardi*.

The larvae of two species of Cleridae, Coleoptera, preyed on the larvae of *C. packardi* in the hypanthium. The mature predators crawled free in hip jars. They are members of the genera *Phyllobaenus* and *Enoclerus*(?). Small numbers of solitary ectoparasites—the ichneumonid,

Scambus hispae and the euplophid, *Euderus cushmani*—attacked the larvae of *packardi* in the hips.

Three solitary endoparasites of the larvae of *Cydia packardi* were discovered. Of these I know two only as first instars; one is probably a species of *Ascogaster*, Braconidae; the other I call the "long-tailed parasite." The third is the ichneumonid, *Glypta rufiscutellaris*, most numerous of the three. *Glypta* attacks also the oriental fruit moth, *Cydia molesta*, and many other lepidopterous larvae living in concealment in plants. The number of cycles developed in a year is said to coincide with that of the host. The terebra is inserted into the openings to the host's burrow, and the egg placed in the small instars of the host. The mature parasite leaves the dead host and pupates in a cocoon.

The rose curculio, *Rhynchites bicolor bicolor*, Curculionidae, Coleoptera, of the eastern United States, prepares an egg pit in the hypanthium, and through it, usually places the egg on the superficial achenes in the hip. The larvae eat the seeds, appearing to shun the achene shells or pericarps. The mature larva drops to the ground and forms a cell which serves as a hibernaculum and, in the spring, for pupation. The adults issue from the ground in May and June when the new crop of hips is developing.

The life stages of *Rhyn. bicolor wickhami*, investigated by Hoerner (1936) in Colorado, are distributed seasonally like those of *bicolor bicolor*. However, the female *wickhami* places the eggs in rose buds, and the larvae feed and develop in the mummified buds. Observers of *Rhyn. bicolor* vars. in areas of northwestern America have reported locations of the eggs and larvae that differ, in some cases, from those described by Hoerner for Colorado and Balduf for Illinois.

Chaetogaster sp.—an oligochaete annelid worm—was found associated with the pupae of *Rhyn. bicolor* in Illinois in a manner that suggests a parasitic relation.

Ectoparasites of Rhyn. bicolor. Four species of solitary ectoparasitic Hymenoptera were reared in small numbers that attacked the larvae of *bicolor* in hips in Illinois. These are *Bracon mellitor* and *B. variabilis*, Braconidae, which are reported to paralyze the host before oviposition; and *Zatropis rosaecolis*, Pteromalidae, and *Eurytoma* sp., Eurytomidae. All pupate in the rose hips near the remnants of the host.

The ichneumonid, *Luchatema baldufi*, is the most numerous parasite of *Rhyn. bicolor* in the Midwest. It is solitary and endoparasitic in the larva. The terebra is inserted through the egg pit made by the female beetle, and the egg deposited in the small instars of the host. Only the first instar is present while the host feeds in the hip and winters in the soil. The parasite appears to complete its first molt when the host is about to prepupate in spring, and quickly completes its larval growth,

destroying the host before it can pupate. The parasite pupates in the host's hibernaculum, and the adults emerge from the ground in June and July when the young host larvae again occur in the new hips.

The rose seed chalcids—Torymidae, *Megastigmus aculeatus*, native to Europe, and *M. nigrovariegatus*, the American species, are very similar in their relations to rose hips. The long terebras penetrate the hypanthium and the then still soft-walled achene, and place the egg in the soft pulpy seed. Here the larvae feed and develop during June and July; the mature larvae occupy the achenes through the fall and winter. Pupation is an event of May and June, and the adults chew out through the pericarp of the achene and the overlying hypanthium. The achenes in the new hips are attacked chiefly in late June and July.

Adults of an *Eupelmus* sp. found dead in a few achenes of *R. rugosa* at Urbana were the only parasites obtained from *Megastigmus*. It appeared to be a very infrequent parasite on the larva of *M. nigrovariegatus*.

Two species of scavengers were discovered, both in only a few instances. The puparia of *Lonchaea polita*, Lonchaeidae, occurred in vacated burrows of *Rhag. basiola* and *Cydia packardi* in old hips in jars, and adults were reared from same. The acarine mite, *Caloglyphus spinitarsus*, developed on dead larvae of *Rhyn. bicolor* and remnants of the parasite, *Luchatema baldufi*, in the hibernacula of the beetle.

Rhag. basiola and its endoparasites, *Opius* and *Halticoptera*, have strictly univoltine life cycles, as do also *Rhyn. bicolor* and its endoparasite *Luchatema*, and the seed chalcids, *Megastigmus* spp. All also exhibit more or less prolonged diapauses—*Rhag. basiola* as an early phase pupa in the puparium, *Opius* spp. as mature larvae in the host puparia, and *Halticoptera* as a mature first instar in the wintering phase pupa of the host fly. *Rhyn. bicolor* diapauses as a mature larva, and its parasite, *Luchatema*, as a mature first instar in the wintering mature host larva. Both species of *Megastigmus* diapause as mature larvae from August to the next May in the achene shells in the hip. A small percentage of *M. nigrovariegatus* pupated precociously.

The above phytophags and their parasites, so far as now known, seem obligated to the rose hip and their rose-hip-inhabiting hosts, respectively. By contrast, *Cydia packardi* develops in the fruits of various plant groups besides *Rosa*, and its principal endoparasite, *Glypta*, likewise utilizes a number of hosts other than *C. packardi*. The number of generations developed in a year by both *Cydia* and *Glypta* is not uniform throughout their geographical range. Also *Bracon mellitor* and *B. variabilis*, ectoparasites on larvae of *Rhyn. bicolor*, attack other hosts of similar habit, and develop at varying rates in the over-all area of their occurrence.

ROSE HOSTS OF HIP INSECTS

<i>Rosa acicularis</i> Lindl.	<i>Rosa nutkana</i> Presl.
<i>Rosa acicularis bourgeauiana</i> Crep.	<i>Rosa oxyodon</i> Boiss.
<i>Rosa acicularis engelmanni</i> Crep.	<i>Rosa palustris</i> Marsh
<i>Rosa alcea</i> Greene	<i>Rosa parviflora</i> Ehrh.
<i>Rosa alpina</i> L. (= <i>pendulina</i> L.)	<i>Rosa pomifera</i> Herrm.
<i>Rosa arkansana</i> Porter	<i>Rosa pyrifera</i> Rydb.
<i>Rosa arkansana suffulta</i> (Greene) Cock.	<i>Rosa rubrifolia</i> R. Br.
<i>Rosa blanda</i> Ait.	<i>Rosa rugosa</i> Thunb.
<i>Rosa blanda glandulosa</i> Schuette	<i>Rosa rugosa kamtschatica</i> (Vent.) Regel
<i>Rosa californica</i> Ch. and Schl.	<i>Rosa sempervirens</i> L.
<i>Rosa calocarpa</i> Willm.	<i>Rosa sericea</i> Lindl.
<i>Rosa canina</i> L.	<i>Rosa setigera</i> Michx.
<i>Rosa carolina</i> L.	<i>Rosa spaldingii</i> Crepin
<i>Rosa carolina villosa</i> L.	<i>Rosa spinosissima</i> L.
<i>Rosa Chaberti</i> Desegl.	<i>Rosa suffulta</i> Greene
<i>Rosa cinnamomea</i> L.	<i>Rosa ultramontana</i> (S. Wats.) Heller
<i>Rosa davurica</i> Pall.	<i>Rosa villosa</i> L.
<i>Rosa eglanteria</i> L. (= <i>rubiginosa</i> L.)	<i>Rosa virginiana</i> Mill.
<i>Rosa gallica</i> L.	<i>Rosa virginica</i> Roess.
<i>Rosa gallica damascena</i> Voss.	<i>Rosa woodsii</i> Lindl.
<i>Rosa gymnocarpa</i> Nutt.	<i>Rosa xanthina</i> Lindl.
<i>Rosa hugonis</i> Hemsl.	<i>Rosa</i> spp.
<i>Rosa jundzilli</i> Bess.	Appendix
<i>Rosa lucida</i> Ehrh.	<i>Rosa alpina</i> var. <i>pyrenaica</i> (?)
<i>Rosa lunellii</i> Greene	<i>Rosa canina</i> vars.
<i>Rosa Macounii</i> Greene	<i>Rosa dumetorum</i> (?)
<i>Rosa macrantha</i> Desf.	<i>Rosa feneliensis</i> (?)
<i>Rosa mollis</i> Smith	<i>Rosa glauca</i> (?)
<i>Rosa mollissima</i> Willd.	<i>Rosa hugonis platyacantha</i> (?)
<i>Rosa Moyesii</i> Hemsl. and Wils.	<i>Rosa medwedewii</i> (?)
<i>Rosa multibracteata</i> Hemsl. and Wils.	<i>Rosa moschata alba</i> (?)
<i>Rosa multiflora</i> Thunb.	<i>Rosa Selongiana</i> (?)
<i>Rosa nitida</i> Willd.	<i>Rosa swenginzowii</i> (?)

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PLATES

PLATE I. *Rhagoletis basiola*

1. Adult. 2. Egg. 3. Right wing.

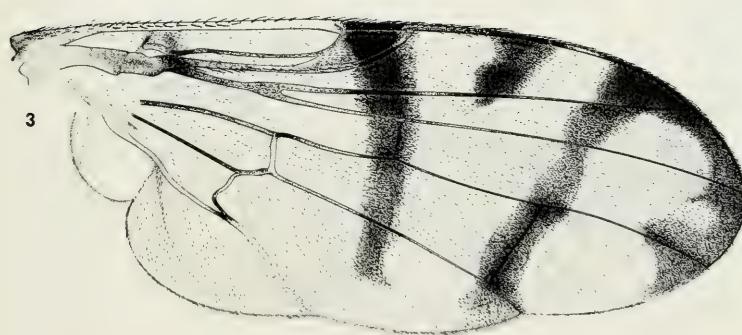
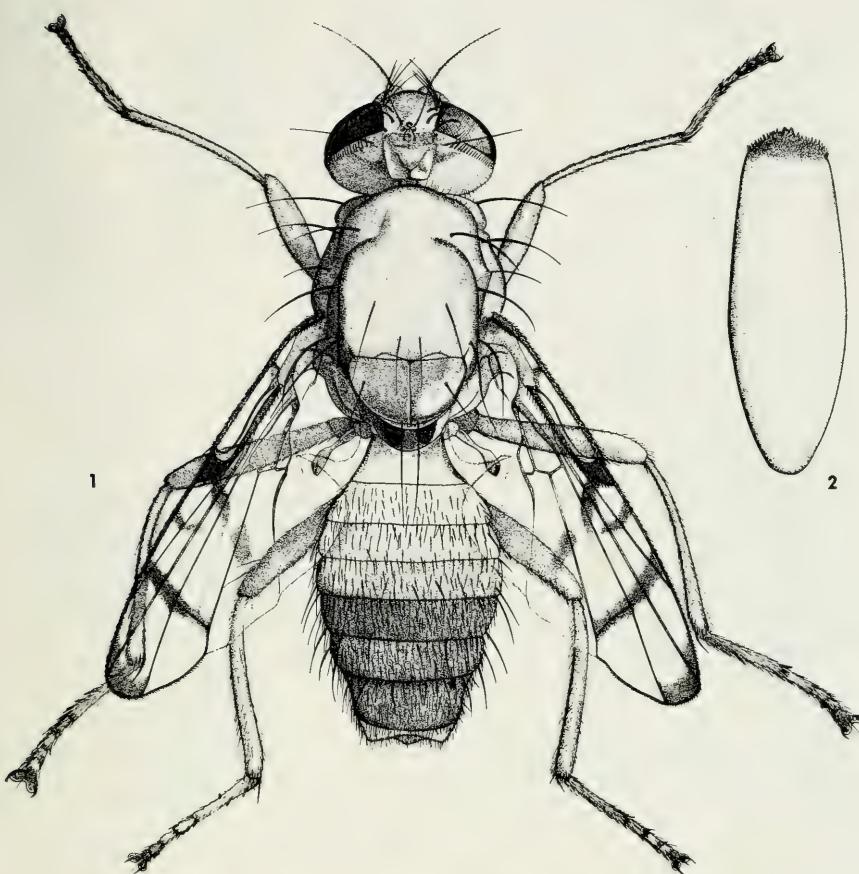


PLATE II. LARVAL STRUCTURES OF *Rhagoletis basiola*

4. Posterior respiratory apparatus of first instar:
a, external dorsocaudal view of spiracular plate; b, atrium; c, trachea.
5. Same of second instar.
6. Posterior spiracular plate of second instar.
7. Posterior spiracular plate of third instar visible within advanced second instar.
8. Mouth hooks of first instar, with connecting structure broken apart.
9. Anterior respiratory "fan" of second instar.
10. Mouth hook of second instar, lateral view, also showing food channels, i.e., "stomal sieves."
11. Cephalic part of oral armature of first instar, in profile:
a, hypostomium.
12. Same of second instar: a, hypostomium; b, parastomium; c, subhypostomium.
13. Same of third instar: a, b, and c, as in Fig. 12.

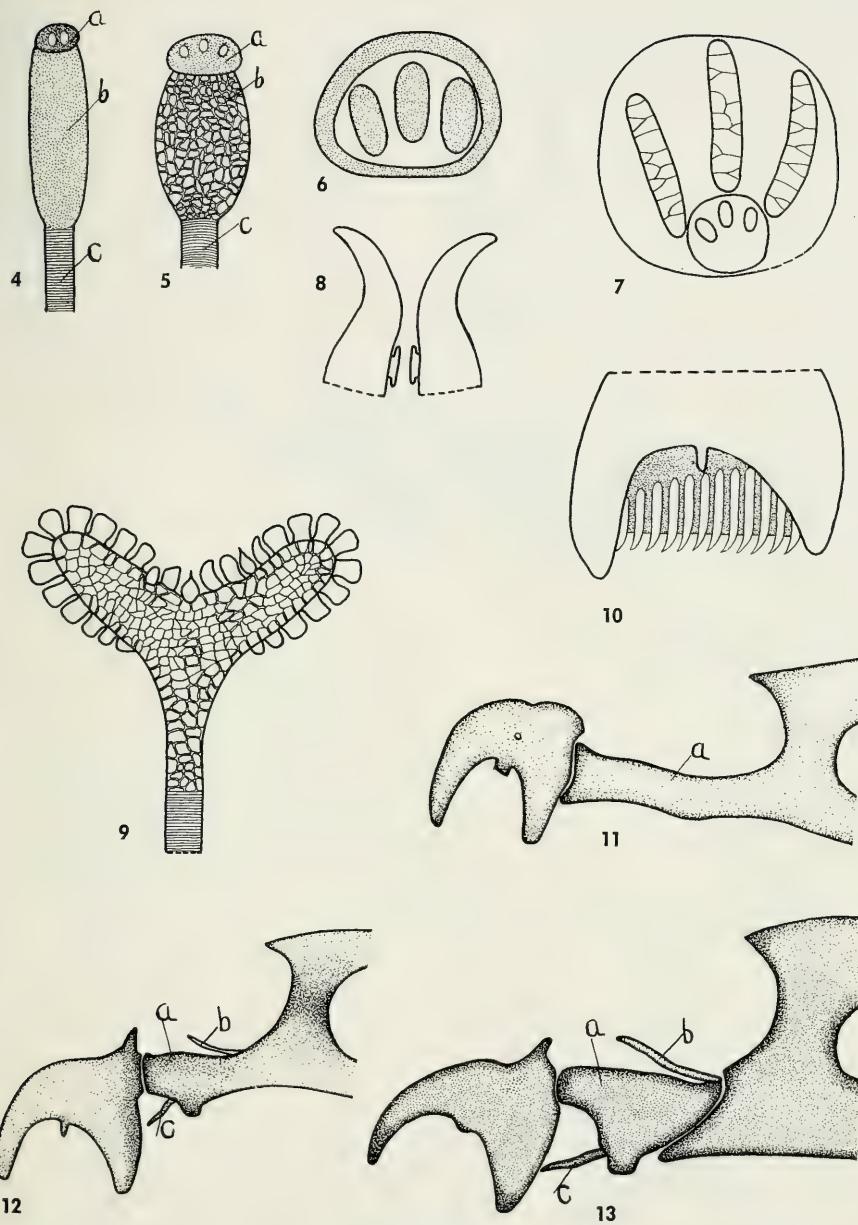


PLATE III. *Opius rosicola* AND *O. baldufi*

14. Adult female of *O. rosicola*.
15. Right wings of *O. baldufi*.
16. Egg of *Opius rosicola* or *baldufi*.
17. First instar of *Opius rosicola* or *baldufi*, dorsolateral view.
18. Second instar of *Opius rosicola* or *baldufi*.

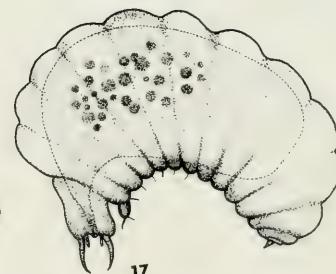
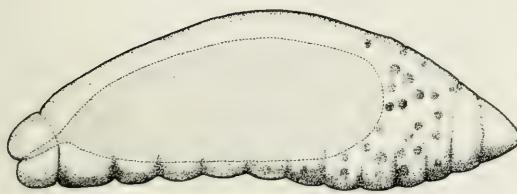
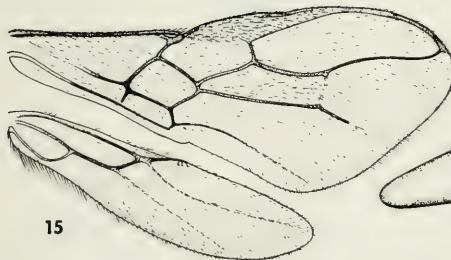
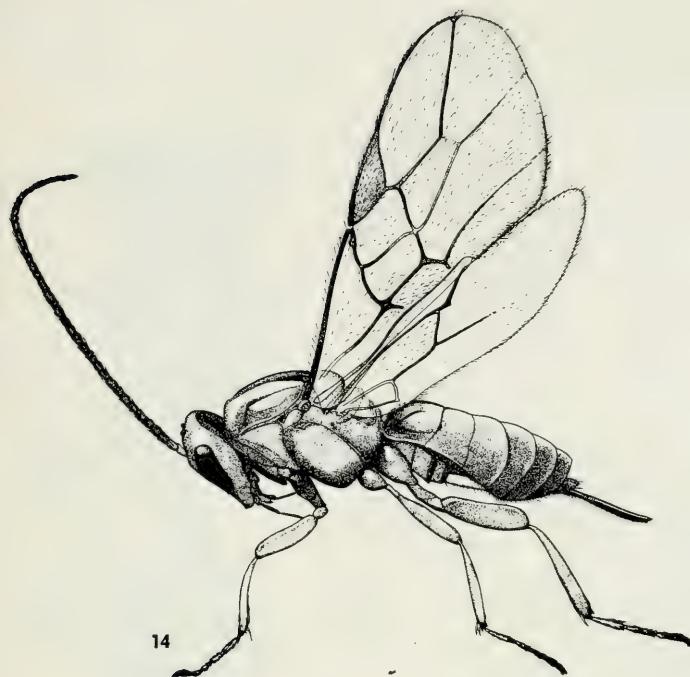
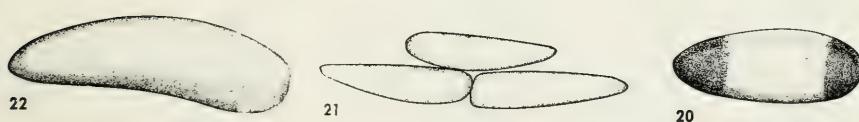


PLATE IV. *Halticoptera rosae*

- 19. Adult.
- 20 and 21. "Brown bodies," or dead eggs.
- 22. Egg.



19



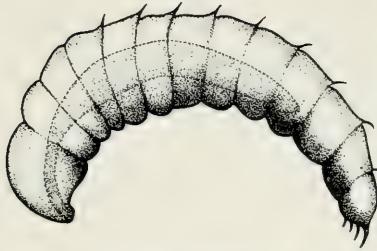
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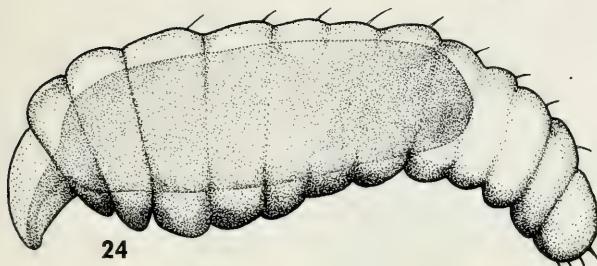
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PLATE V. *Halticoptera rosae*

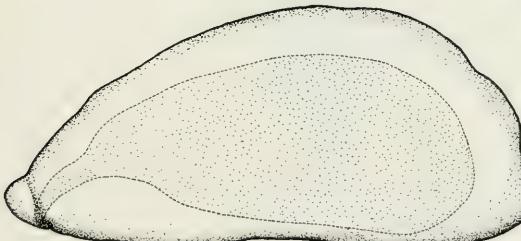
- 23. Early phase of first instar.
- 24. Intermediate phase of same.
- 25. Advanced phase of same.
- 26. Second instar.
- 27. Mature larva.



23



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PLATE VI. *Glypta rufiscutellaris*

28. Adult female of *Glypta rufiscutellaris* in profile.

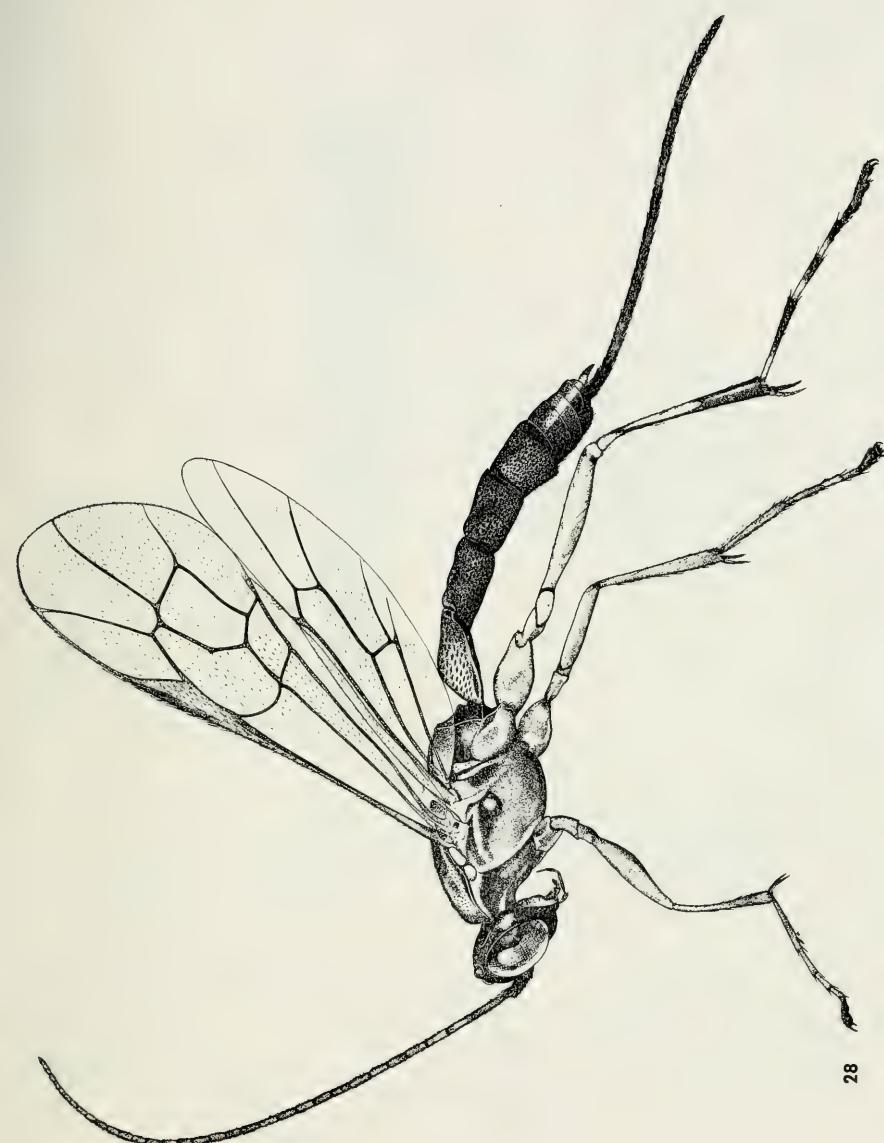


PLATE VII. *Glypta rufiscutellaris.*

29. Adult male of *Glypta rufiscutellaris.*
30. First instar of same, lateral view.
31. Second instar of same, lateral view.
32. Egg of *Glypta rufiscutellaris.*

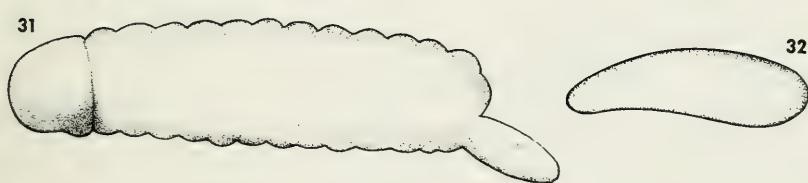
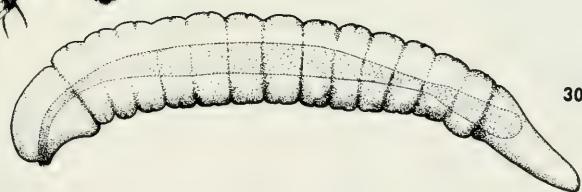
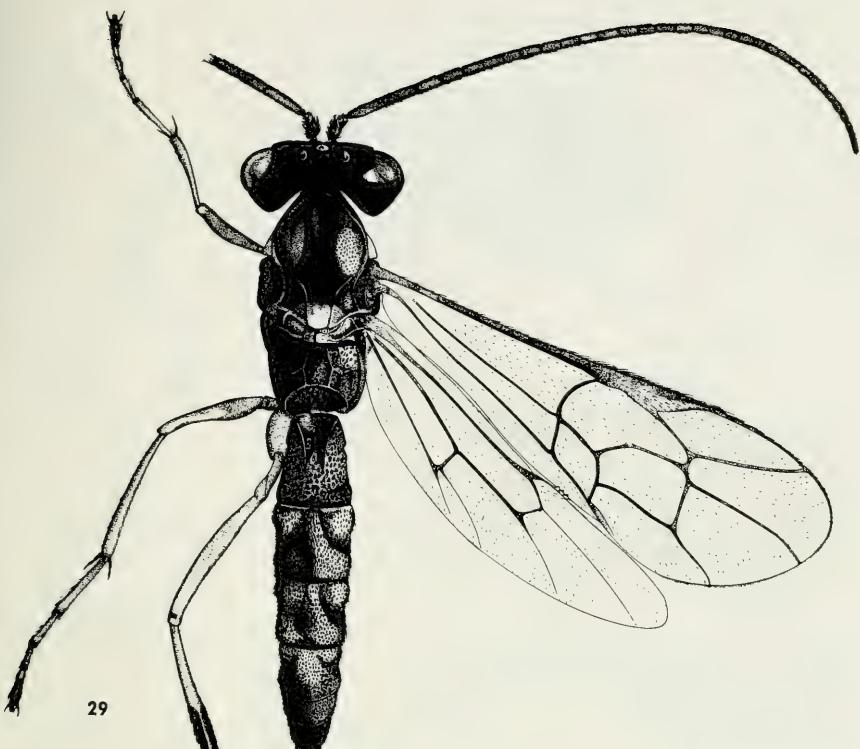
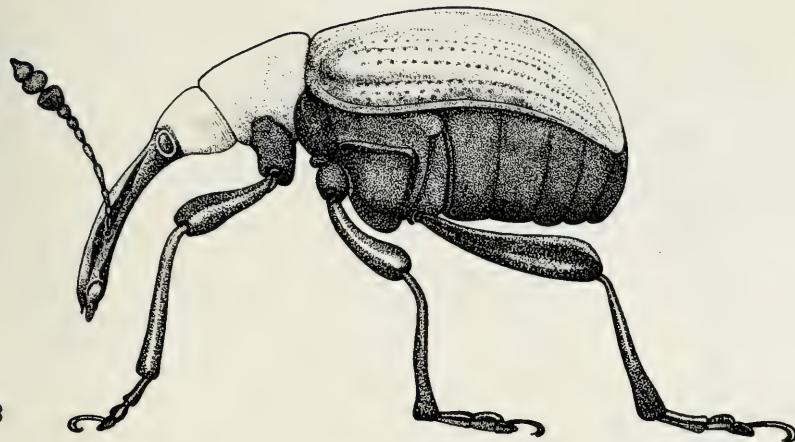


PLATE VIII. *Rhynchites bicolor*

- 33. Adult of *Rhynchites bicolor*, lateral view.
- 34. Egg of same, dorsal view.
- 35. Egg of same, lateral view.
- 36. Mature larva of same, lateral view.
- 37. Pupa of same, ventral view.
- 38. Pupa of same, dorsal view.



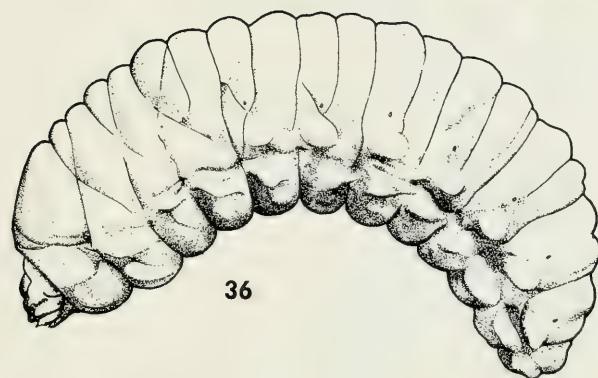
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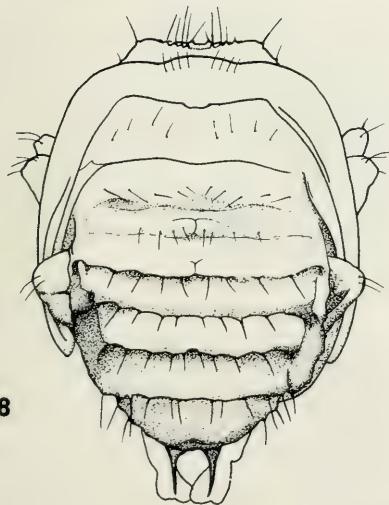
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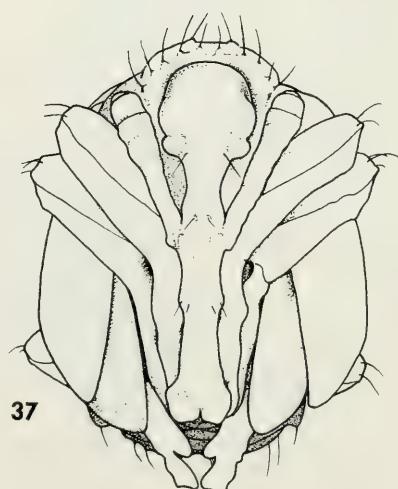
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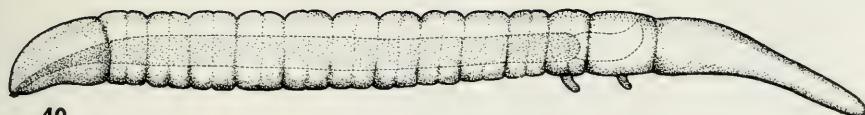
PLATE IX. *Luchatema baldufi*

39. Adult female of *Luchatema baldufi*, in profile.

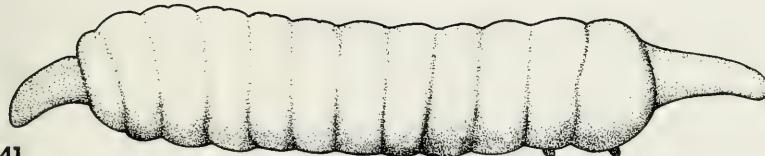


PLATE X. *Luchatema baldufi*

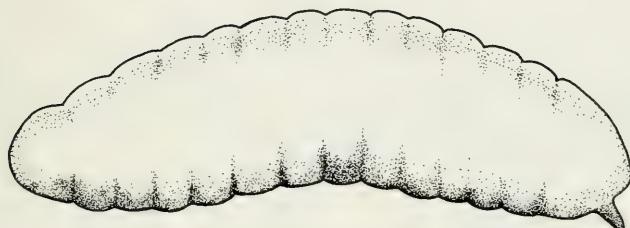
40. Early phase of first instar, lateral view.
41. Advanced phase of same.
42. Second instar.
43. Mature larva.
44. Egg.
45. Cocoon, showing position of larval excrement (a).



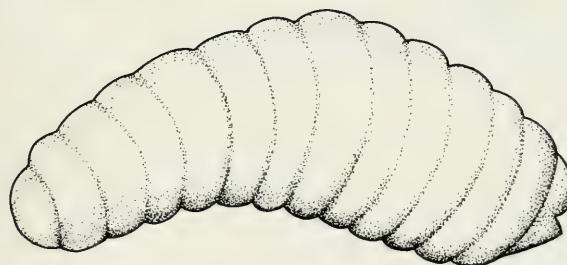
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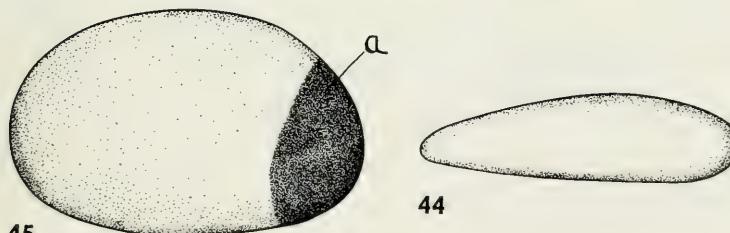
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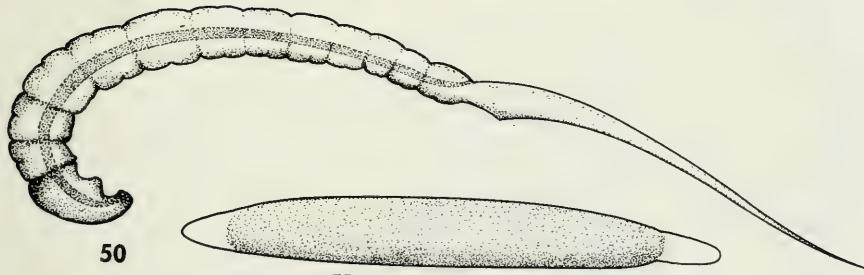
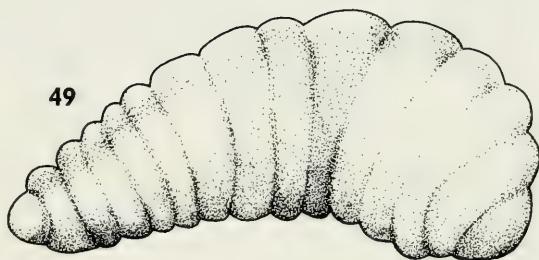
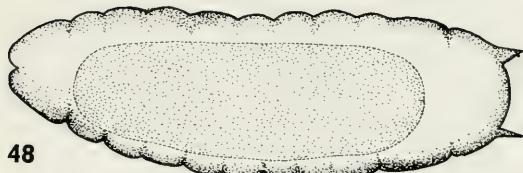
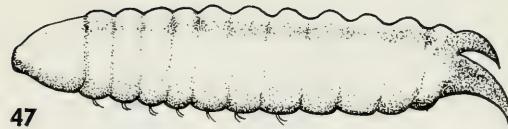
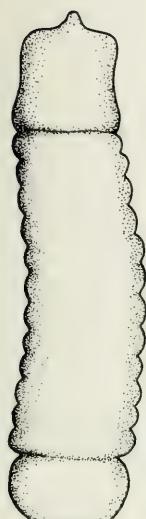


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PLATE XI. *Parasites*

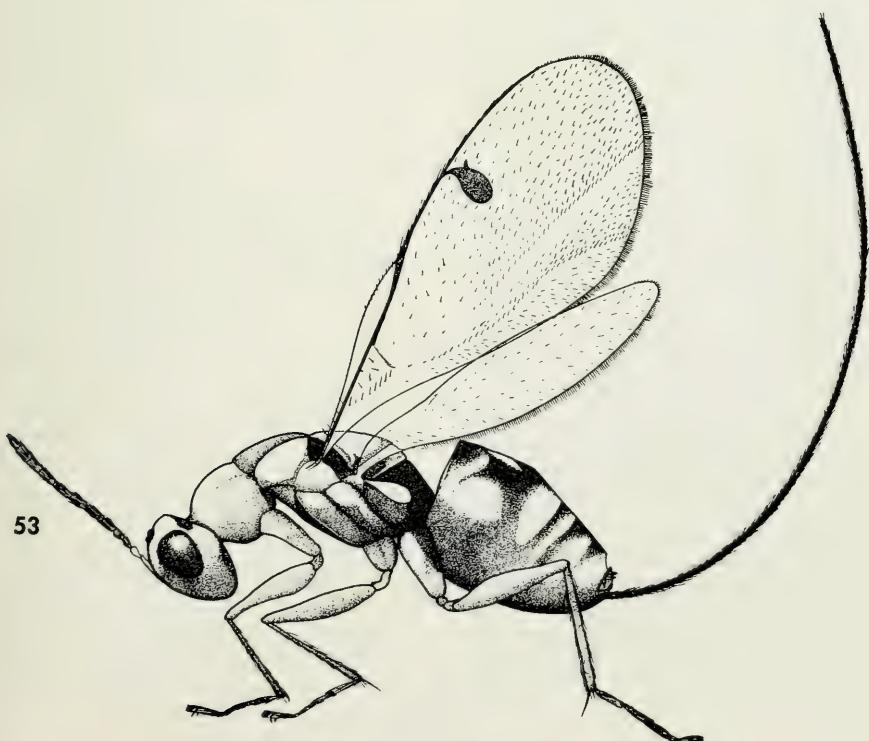
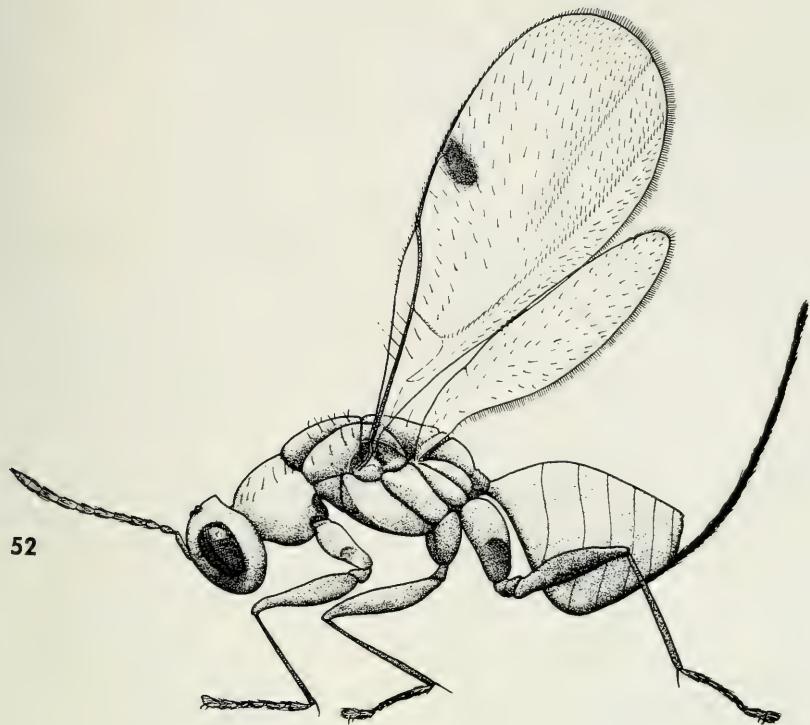
46. First instar of *Ascogaster* sp. from *Cydia packardi*.
47. First instar of eupelmid? from *Rhag. basiola*, dorsolateral view.
48. Supposed second instar of eupelmid? from *Rhag. basiola*, dorsal view.
49. Full-grown larva of *Zatropis rosaecolis*, on *Rhynchites bicolor*.
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51. Egg of a parasite, presumably on *Cydia packardi*.



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PLATE XII. *Megastigmus*

52. Female of *Megastigmus nigrovariegatus* Ashmead. The American rose seed chalcid.
53. Female of *Megastigmus aculeatus* (Swed.). European rose seed chalcid.



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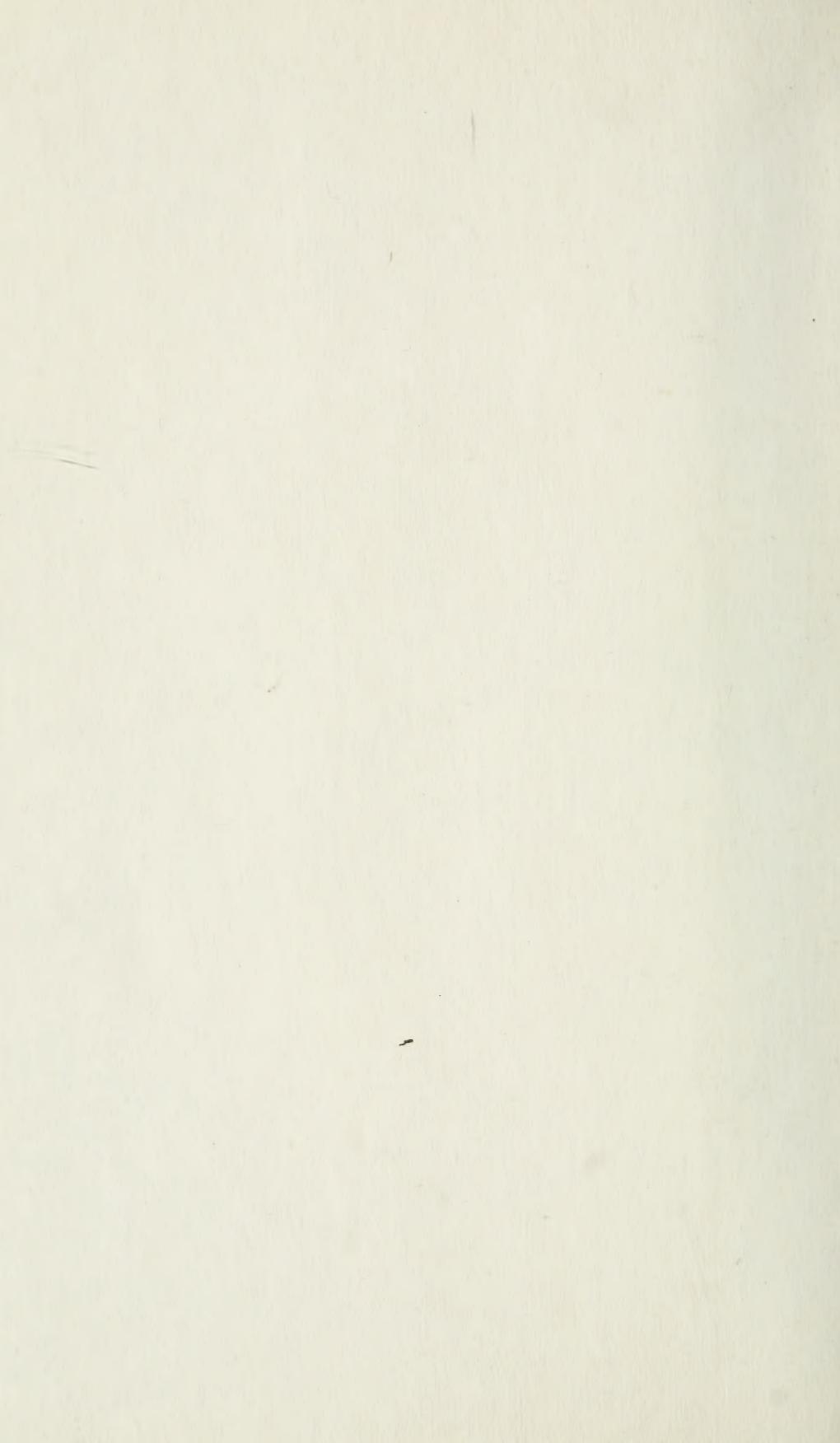
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